LESSONS

IN

ELEMENTARY PHYSIOLOGY

Cm. Calcaneum.
As. Astragalus.
N. Naviculare.

C^1, C^2, C^3. The three Cuneiform bones
Cb. The Cuboid.

HUXLEY'S PHYSIOLOGY.

LESSONS
IN ELEMENTARY
PHYSIOLOGY

BY

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PREFACE

In approaching the revision of "Huxley's Physiology," my feelings have been similar to those of an architect to whom is entrusted the restoration of a historic building designed by a master hand.

Written by Huxley, the book was revised, and in fact almost rewritten, by Foster. The former was as great a writer as any scientist of his time, the latter may almost be said to have created English Physiology.

To "restore" the work of these men from the dilapidations made by two decades of scientific progress is the task now entrusted to me. The sense of responsibility with which I approach it is, if possible, heightened by the affection which I have for the memory of Foster, who was my master.

I have faithfully left untouched any portion of the fabric in which there was not an actual flaw;

but where the structure needed repair, it seemed to me due not only to the readers of the book but to the memory of the author, that the repair should be thorough, substantial, and simple. Such have been the principles on which I have tried to carry out my work. I have been greatly helped by Mrs. Thacker, Fellow of Newnham College, who has read through my proofs, and made valuable suggestions.

JOSEPH BARCROFT.

KING'S COLLEGE, CAMBRIDGE,
November 24, 1914.

CONTENTS

LESSON I

A GENERAL VIEW OF THE STRUCTURE AND FUNCTIONS OF THE HUMAN BODY. Pp. 3–29

LESSON II

THE ORGANS OF CIRCULATION. Pp. 30—92

PART I.—THE BLOOD VASCULAR SYSTEM AND THE CIRCULATION

LESSON VIII

LESSON IX

LESSON X

THE COALESCENCE OF SENSATIONS WITH ONE ANOTHER AND WITH OTHER STATES OF CONSCIOUSNESS. Pp. 437–451

LESSON XI

THE NERVOUS SYSTEM AND INNERVATION. Pp. 452–534

LESSON XII

HISTOLOGY; OR, THE MINUTE STRUCTURE OF THE TISSUES. Pp. 535—560

APPENDIX

ANATOMICAL AND PHYSIOLOGICAL CONSTANTS

LIST OF ILLUSTRATIONS

LESSONS

IN

ELEMENTARY PHYSIOLOGY

A COMPARISON OF CERTAIN BRITISH AND METRIC UNITS.

Thermometric.

Centigrade.	Fahrenheit.
0°	32°
5	41
10	50
15	59
20	68
25	77
30	86
35	95
36	96·8
37	98·6
38	100·4
39	102·2
40	104
41	105·8
42	107·6
43	109·4
44	111·2
45	113
55	131
65	149
75	167
85	185
95	203
100	212

Length ...
- 1 meter (m.) = 1000 millimeters (mm.).
- = 100 centimeters (cm.) = 39·37 inches.
- 1 inch = 25·4 millimeters.
- 1 foot = 30·4 centimeters.
- $\mu = \frac{1}{1000}$ millimeter = $\frac{1}{25000}$ inch (nearly).

Weight ...
- 1 kilogramme (kg.) = 1000 grammes (g.) = 2·2 lbs. Avoir.
- 1 gramme (g.) = 1000 milligrammes (mg.) = 15·4 grains.
- 1 pound (Avoir.) = 453·6 grammes, or about ½ kilogramme.
- 1 ounce ,, = 28·35 grammes = 437·5 grains.

Capacity..
- 1 litre (l.) = 1000 cubic centimeters (c.c.) = 1·76 pint.
- 1 fluid ounce = 28·4 cubic centimeters.
- 1 pint = 20 fluid oz. = 567·5 cubic centimeters.
- 1 gallon = 4·54 litres.
- 1 cubic inch = 16·38 cubic centimeters
- 1 cubic foot = 28·3 litres.

Work ......
- 1 kilogramme-meter (kg.m.) = 7·25 foot-pounds
- 1 foot-pound = ·138 kilogramme-meter.
- 1 foot-ton = 310 kilogramme-meters.

Heat ......
- (British) 1 unit of heat = heat necessary to raise 1 pound of water through 1° F.
- (Metric) 1 calorie = ,, ,, ,, ,, 1 gramme ,, 1° C.
- Mechanical equivalent of heat unit = 772 foot-pounds.
- ,, ,, ,, calorie = 424 gramme-meters.

LESSONS

IN

ELEMENTARY PHYSIOLOGY

LESSON I

A GENERAL VIEW OF THE STRUCTURE AND FUNCTIONS OF THE HUMAN BODY

1. **The Work of the Body as a whole.**—The body of a living man performs a great diversity of actions, some of which are quite obvious; others require more or less careful observation; and yet others can be detected only by the employment of the most delicate appliances of science.

Thus, some part of the body of a living man is plainly always in motion. Even in sleep, when the limbs, head, and eyelids may be still, the incessant rise and fall of the chest continue to remind us that we are viewing slumber and not death.

More careful observation, however, is needed to detect the motion of the heart; or the pulsation of the arteries; or the changes in the size of the pupil of the eye with varying light; or to ascertain that the air which is breathed

out of the body is hotter and damper than the air which is taken in by breathing.

And lastly; when we try to ascertain what happens in the eye when that organ is adjusted to different distances; or what in a nerve when it is excited: or of what materials flesh and blood are made: or in virtue of what mechanism it is that a sudden pain makes one start—we have to call into operation all the methods of inductive and deductive logic; all the resources of physics and chemistry; and all the delicacies of the art of experiment.

The sum of the facts and generalizations at which we arrive by these various modes of inquiry, be they simple or be they refined, concerning the actions of the body and the manner in which those actions are brought about, constitutes the science of Human Physiology. An elementary outline of this science, and of so much anatomy as is incidentally necessary, is the subject of the following Lessons; of which we shall devote the present to an account of so much of the structure and such of the actions (or, as they are technically called, "functions") of the body, as can be ascertained by easy observation; or might be so ascertained if the bodies of men were as easily procured, examined, and subjected to experiment, as those of animals.

Suppose a chamber with walls of ice, through which a current of pure ice-cold air passes; the walls of the chamber will of course remain unmelted.

Now, having weighed a healthy living man with great care, let him walk up and down the chamber for an hour. In doing this he will obviously do a considerable amount of work and use up a proportionate quantity of energy; as much, at least, as would be required to lift his weight as high and as often as he has raised himself at every step. But, in addition, a certain quantity of the ice will be melted, or converted into water; showing that the man has given off heat in abundance. Furthermore, if the air which enters the chamber be made to pass through lime-water, it will cause no cloudy white precipitate of car-

bonate of lime, because the quantity of carbonic acid[1] in ordinary air is so small as to be inappreciable in this way. But if the air which passes out is made to take the same course, the lime-water will soon become milky, from the precipitation of carbonate of lime, showing the presence of carbonic acid, which, like the heat, is given off by the man.

Again, even if the air be quite dry as it enters the chamber (and the chamber be lined with some material so as to shut out all vapour from the melting ice walls), that which is breathed out of the man, and that which is given off from his skin, will exhibit clouds of vapour; which vapour, therefore, is derived from the body.

After the expiration of the hour during which the experiment has lasted, let the man be released and weighed once more. He will be found to have lost weight.

Thus a living, active man, constantly does **mechanical work**, gives off **heat**, evolves **carbonic acid** and **water**, and undergoes a **loss of substance**.

Plainly, this state of things could not continue for an unlimited period, or the man would dwindle to nothing. But long before the effects of this gradual diminution of substance become apparent to a bystander, they are felt by the subject of the experiment in the form of the two imperious sensations called hunger and thirst. To still these cravings, to restore the weight of the body to its former amount, to enable it to continue giving out heat, water, and carbonic acid, at the same rate, for an indefinite period, it is absolutely necessary that the body should be supplied with each of three things, and with three only. These are, firstly, fresh air; secondly, drink—consisting of water in some shape or other, however much it may be adulterated; thirdly, food. That compound known to

[1] By "carbonic acid" we mean "carbonic acid gas." This should in strictness be called carbon dioxide (CO_2), carbonic acid being the compound of this with water, H_2CO_3. But for simplicity's sake, and because the expression "carbonic acid" is in general use and is generally understood to stand for carbon dioxide, we shall use it throughout this book.

chemists as **Protein** matter (Lesson III.), and which contains carbon, hydrogen, oxygen, nitrogen, and sulphur, must form a part of this food, if it is to sustain life indefinitely; and fatty, starchy, or saccharine, *i.e.* carbohydrate matters, together with a certain amount of salts, ought to be contained in the food, if it is to sustain life conveniently.

A certain proportion of the matter taken in as food either cannot be, or at any rate is not, used; and leaves the body, as *excrementitious matter*, having simply passed through the alimentary canal without undergoing much change, and without ever being incorporated into the actual substance of the body. But, under healthy conditions, and when only so much food as is necessary is taken, no important proportion of either protein matter, or fat, or starchy or saccharine food, passes out of the body as such. Almost all real food ultimately leaves the body as waste in the form either of **water**, or of **carbonic acid**, or of a third substance called **urea**, or of certain saline compounds or **salts**.

Chemists have determined that these products which are thrown out of the body and are called **excretions**, contain if taken altogether, far more oxygen than the food and water taken into the body. Now, the only possible source whence the body can obtain oxygen, except from food and water, is the air which surrounds it.[1] And careful investigation of the air which leaves the chamber in the imaginary experiment described above would show, not only that it has gained carbonic acid *from* the man, but that it has lost *oxygen* in equal or rather greater amount *to* him.

Thus, if a man is neither gaining nor losing weight, the sum of the weights of all the substances above enumerated which leave the body ought to be exactly equal to the

[1] Fresh country air contains in every 100 parts nearly 21 of oxygen and 79 of nitrogen gas, together with a small fraction of a part (·04) of carbonic acid, and a variable quantity of watery vapour. The constituent of the atmosphere, argon, present in small quantities, is here reckoned in with the nitrogen. (See Lesson IV.)

weight of the food and water which enter it, together with that of the oxygen which it absorbs from the air. And this is proved to be the case.

Hence it follows that a man in health, and "neither gaining nor losing flesh," is *incessantly* oxidating and wasting away, and *periodically* making good the loss. So that if, in his average condition, he could be confined in the scale-pan of a delicate spring balance, like that used for weighing letters, the scale-pan would descend at every meal, and ascend in the intervals, oscillating to equal distances on each side of the average position, which would never be maintained for longer than a few minutes. There is, therefore, no such thing as a stationary condition of the weight of the body, and what we call such is simply a condition of variation within narrow limits—a condition in which the gains and losses of the numerous daily transactions of the economy balance one another.

Suppose this diurnally-balanced physiological state to be reached, it can be maintained only so long as the quantity of the mechanical work done, and of heat, or other force evolved, remains absolutely unchanged.

Let such a physiologically-balanced man lift a heavy body from the ground, and the loss of weight which he would have undergone without that exertion will be increased by a definite amount, which cannot be made good unless a proportionate amount of extra food be supplied to him. Let the temperature of the surrounding air fall, and the same result will occur, if his body remains as warm as before.

On the other hand, diminish his exertion and lower his production of heat, and either he will gain weight, or some of his food will remain unused.

Thus, in a properly nourished man, a stream of food is constantly entering the body in the shape of complex compounds containing comparatively little oxygen; as constantly, the elements of the food (whether before or

after they have formed part of the living substance) are leaving the body, combined with more oxygen. And the incessant breaking down and oxidation of the complex compounds which enter the body are definitely proportioned to the amount of energy the body gives out, whether in the shape of heat or otherwise; just in the same way as the amount of work to be got out of a steam-engine, and the amount of heat it and its furnace give off, bear a strict proportion to its consumption of fuel.

From these general considerations regarding the nature of life, considered as physiological work, we may turn for the purpose of taking a like broad survey of the apparatus which does the work. We have seen the general performance of the engine, we may now look at its build.

2. The General Build of the Body.—The human body is obviously separable into **head**, **trunk**, and **limbs**. In the head, the brain-case or **skull** is distinguishable from the **face**. The trunk is naturally divided into the chest or **thorax**, and the belly or **abdomen**. Of the limbs there are two pairs—the upper, or **arms**, and the lower, or **legs**; and legs and arms again are subdivided by their joints into parts which obviously exhibit a rough correspondence—**thigh** and **upper arm**, **leg** and **fore-arm**, **ankle** and **wrist**, **fingers** and **toes**, plainly answering to one another. And the two last, in fact, are so similar that they receive the same name of **digits**; while the several joints of the fingers and toes have the common denomination of **phalanges**.

The whole body thus composed (without the viscera or organs which fill the cavities of the trunk) is seen to be bilaterally symmetrical; that is to say, if it were split lengthways by a great knife, which should be made to pass along the middle line of both the dorsal and ventral (or back and front) aspects, the two halves would almost exactly resemble one another.

One-half of the body, divided in the manner described (Fig. 1, A), would exhibit in the trunk, the cut faces of

thirty-three bones, joined together by a very strong and tough substance into a long column, which lies much nearer the *dorsal* (or back) than the *ventral* (or front) aspect of the body. The bones thus cut through are called the *bodies* of the **vertebræ**. They separate a long, narrow canal, called the **spinal canal,** which is placed upon their dorsal side, from the spacious chamber of the chest and abdomen, which lies upon their ventral side. There is no direct communication between the dorsal canal and the ventral cavity.

The spinal canal contains a long white cord—the **spinal cord**—which is an important part of the nervous system. The ventral chamber is divided into the two subordinate cavities of the thorax and abdomen by a remarkable, partly fleshy and partly membranous, partition, the **diaphragm** (Fig. 1, *D*), which is concave towards the abdomen, and convex towards the thorax. The **alimentary canal** (Fig. 1, *Al.*) traverses these cavities from one end to the other, piercing the diaphragm. So does a long double series of distinct masses of nervous substance, which are called **ganglia,** are connected together by nervous cords, and constitute the so-called **sympathetic system** (Fig. 1, *Sy.*). The abdomen contains, in addition to these parts, the two **kidneys**, one placed against each side of the vertebral column and connected each by a tube, the **ureter,** to a muscular bag, the **bladder** lying at the bottom of the abdomen; the **liver,** the **pancreas** or "sweetbread" and the **spleen.** The thorax incloses, besides its segment of the alimentary canal and of the sympathetic, the **heart** and the two **lungs.** The latter are placed one on each side of the heart, which lies nearly in the middle of the thorax.

Where the body is succeeded by the head, the uppermost of the thirty-three vertebral bodies is followed by a continuous mass of bone, which extends through the whole length of the head, and, like the spinal column, separates a dorsal chamber from a ventral one. The dorsal chamber,

or **cavity of the skull,** opens into the spinal canal. It contains a mass of nervous matter called the **brain,** which is continuous with the spinal cord, the brain and the spinal cord together constituting what is termed the **cerebro-spinal system** (Fig. 1, *C.S.*, *C.S.*). The ventral chamber, or **cavity of the face,** is almost entirely occupied by the **mouth**, and **pharynx**, into which last the upper end of the alimentary canal (called gullet or **œsophagus**) opens.

Thus, the study of a longitudinal section shows us that the human body is a double tube, the two tubes being completely separated by the spinal column and the bony axis of the skull, which form the floor of the one tube and the roof of the other. The dorsal tube contains the cerebro-spinal axis ; the ventral tube contains the alimentary canal, the sympathetic nervous system, the heart, and the lungs, besides other organs.

Transverse sections, taken perpendicularly to the axis of the vertebral column, or to that of the skull, show still more clearly that this is the fundamental structure of the human body, and that the great apparent difference between the head and the trunk is due to the different size of the dorsal cavity relatively to the ventral. In the head the former cavity is very large in proportion to the size of the latter (Fig. 1, B) ; in the thorax, or abdomen it is very small (Fig. 1, C).

The limbs contain no such chambers as are found in the body and the head ; but with the exception of certain branching tubes filled with fluid, which are called **blood-vessels** and **lymphatics,** are solid or semi-solid, throughout.

3. The Tissues generally.—Such being the general character and arrangement of the parts of the human body, it will next be well to consider into what constituents it may be separated by the aid of no better means of discrimination than the eye and the anatomist's knife.

With no more elaborate aids than these, it becomes

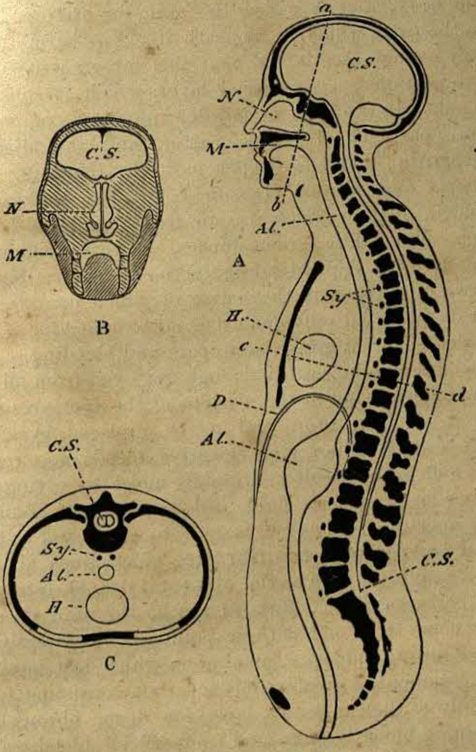

FIG. 1.

A. A diagrammatic section of the human body taken vertically through the median plane. *C.S.* the cerebro-spinal nervous system; *N*, the cavity of the nose; *M*, that of the mouth; *Al. Al.* the alimentary canal represented as a simple straight tube; *H*, the heart; *D*, the diaphragm; *Sy*, the sympathetic ganglia.

B. A transverse vertical section of the head taken along the line *a b*; letters as before.

C. A transverse section taken along the line *c d*; letters as before.

easy to separate that tough membrane which invests the whole body, and is called the skin, or **integument**, from the parts which lie beneath it. Furthermore, it is readily enough ascertained that this integument consists of two portions: a superficial layer, which is constantly being shed in the form of powder or scales composed of minute particles of horny matter, and is called the **epidermis**; and the deeper part, the **dermis**, which is dense and fibrous (Lesson V.). The epidermis, if wounded, neither gives rise to pain nor bleeds. The dermis, under like circumstances, is very tender, and bleeds freely. A practical distinction is drawn between the two in shaving, in the course of which operation the razor ought to cut only epidermic structures; for if it go a shade deeper, it gives rise to pain and bleeding.

The skin can be readily enough removed from all parts of the exterior, but at the margins of the apertures of the body it seems to stop, and to be replaced by a layer which is much redder, more sensitive, bleeds more readily, and which keeps itself continually moist by giving out a more or less tenacious fluid, called **mucus**. Hence, at these apertures, the skin is said to stop, and to be replaced by **mucous membrane**, which lines all those interior cavities, such as the alimentary canal, into which the apertures open. But, in truth, the skin does not really come to an end at these points, but is directly continued into the mucous membrane, which last is simply an integument of greater delicacy, but consisting fundamentally of the same two layers—a deep, fibrous layer, containing blood-vessels, and a superficial bloodless one, now called the **epithelium**. Thus every part of the body might be said to be contained between the walls of a double bag, formed by the epidermis, which invests the outside of the body, and the epithelium, its continuation, which lines the alimentary canal.

The dermis, and the deep, vascular layer, which answers to it in the mucous membranes, are chiefly made up of

a filamentous substance, which yields abundant **gelatine** on being boiled, and is the matter which tans when hide is made into leather. This is called **connective tissue**,[1] because it is the great connecting medium by which the different parts of the body are held together. Thus it passes from the dermis between all the other organs, ensheathing the muscles, coating the bones and cartilages, and eventually reaching and entering into the mucous membranes. And so completely and thoroughly does the connective tissue permeate almost all parts of the body, that if every other tissue could be dissected away, a complete model of all the organs would be left composed of this tissue. Connective tissue varies very much in character; in some places being very soft and tender, at others—as in the tendons and ligaments, which are almost wholly composed of it—attaining great strength and density.

Among the most important of the tissues imbedded in and ensheathed by the connective tissue, are some the presence and action of which can be readily determined during life.

If the upper arm of a man whose arm is stretched out be tightly grasped by another person, the latter, as the former bends up his fore-arm, will feel a great soft mass which lies at the fore part of the upper arm, swell, harden, and become prominent. As the arm is extended again, the swelling and hardness vanish.

On removing the skin, the body which thus changes its configuration is found to be a mass of red flesh, sheathed in connective tissue. The sheath is continued at each end into a tendon, by which the muscle is attached, on the one hand, to the shoulder-bone, and, on the other, to one of the bones of the fore-arm. This mass of flesh is the **muscle** called *biceps*, and it has the peculiar property of changing its dimensions—shortening and becoming thick in proportion to its decrease in length—when

[1] Every such constituent of the body, as epidermis, cartilage, or muscle, is called a "tissue." (See Lesson XII.)

influenced by the will as well as by some other causes, called **artificial stimuli**, and of returning to its original form when let alone. This temporary change in the dimensions of a muscle, this shortening and thickening, is spoken of as its **contraction**. It is by reason of this property that muscular tissue becomes the great motor agent of the body ; the muscles being so disposed between the systems of levers which support the body, that their contraction necessitates the motion of one lever upon another.

4. The Skeleton.—These levers form part of the system of hard tissues which constitute the **skeleton**. The less hard of these are the **cartilages**, composed of a dense, firm substance, ordinarily known as "gristle." The harder are the **bones**, which are masses of tissue, hardened by being impregnated with **phosphate** and **carbonate of lime**. They are animal tissues which have become, in a manner, naturally petrified ; and when the salts of lime are extracted, as they may be, by the action of acids, a model of the bone in soft and flexible animal matter remains.

More than 200 separate bones are ordinarily reckoned in the human body, though the actual number of distinct bones varies at different periods of life, many bones which are separate in youth becoming united together in old age. Thus there are originally, as we have seen, thirty-three separate bodies of vertebræ in the spinal column, and the upper twenty-four of these commonly remain distinct throughout life. But the twenty-fifth, twenty-sixth, twenty-seventh, twenty-eighth, and twenty-ninth early unite into one great bone, called the **sacrum** ; and the four remaining vertebræ often run into one bony mass called the **coccyx**.

In early adult life, the skull contains twenty-two naturally separate bones, but in youth the number is much greater, and in old age far less.

Twenty-four ribs bound the chest laterally, twelve on each side, and most of them are connected by cartilages with

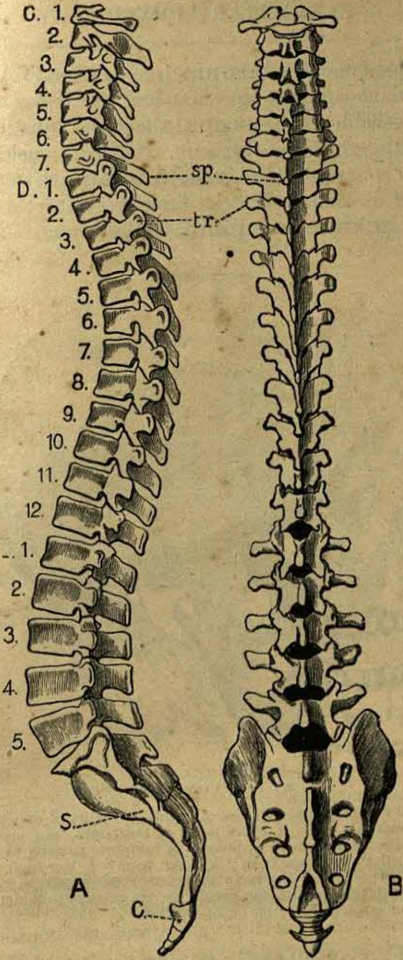

FIG. 2.—THE VERTEBRAL COLUMN.

A, side view, left side; B, back view; C 1-7, cervical vertebræ; D 1-12, dorsal (thoracic) vertebræ; L 1-5, lumbar vertebræ; S, sacrum; C, coccyx; sp, spinous processes; tr, transverse processes.

the breast-bone or **sternum** (see Lesson IV.). In the girdle which supports the shoulder, two bones are always distinguishable as the **scapula** and the **clavicle**. The **pelvis**, to which the legs are attached, consists of two separate bones called the **ossa innominata** in the adult; but each os innominatum is separable into three (called **pubis, ischium,** and **ilium**) in the young.

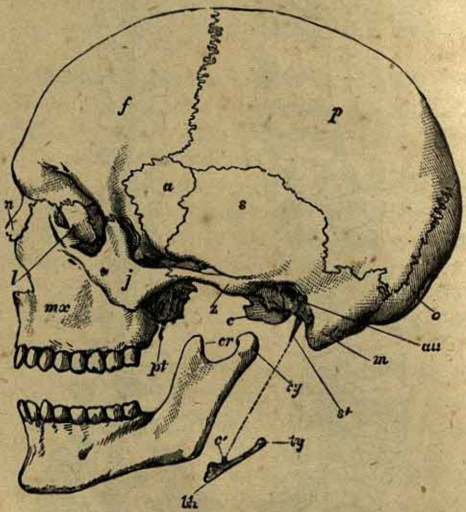

Fig. 3.—Side View of the Skull.

f, frontal bone; *p*, parietal; *o*, occipital; *a*, wing of sphenoid; *s*, flat part of temporal; *c*, *m*, *st*, other parts of temporal; *au*, opening of ear or external auditory canal; *z*, process of temporal passing to *j*, the cheek bone; *mx*, the upper jaw bone; *n*, nasal bone; *l*, lacrymal; *pt*, part of sphenoid. The lower jaw bone is drawn downwards; *cy*, its process which articulates with the temporal; *cr*, its process to which muscles of mastication are attached; *th*, *ty*, hyoid bone.

There are thirty bones in each of the arms, and the same number in each of the legs, counting the **patella,** or knee-cap.

All these bones are fastened together by ligaments, or by cartilages; and where they play freely over one another, a coat of cartilage furnishes the surfaces which come into contact. The cartilages which thus form part of a joint are called **articular** cartilages, and their free surfaces, by which they rub against each other, are lined by a delicate **synovial** membrane, which secretes a lubricating fluid—the **synovia.**

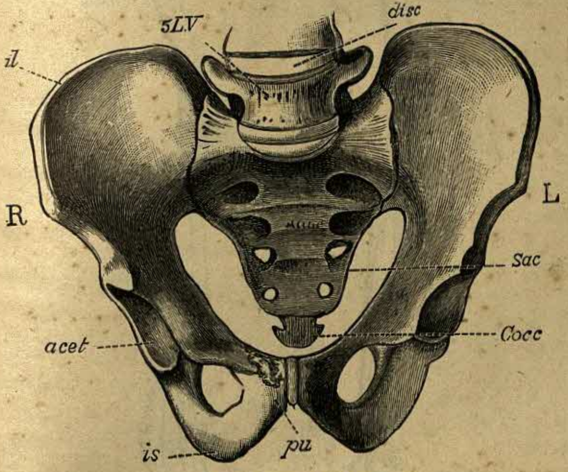

FIG. 4.—THE PELVIS.

Sac. sacrum; *Cocc.* coccyx; *il*, *is*, *pu*, ilium, ischium, pubis, three parts of the innominate or hip bone; *acet*, acetabulum cup for head of femur; *5 L.V*, 5th lumbar vertebra.

5. The Erect Position.—Though the bones of the skeleton are all strongly enough connected together by ligaments and cartilages, the joints play so freely, and the centre of gravity of the body, when erect, is so high up, that it is impossible to make a skeleton or a dead body support itself in the upright position. That position, easy as it seems, is the result of the contraction of a multitude of muscles which

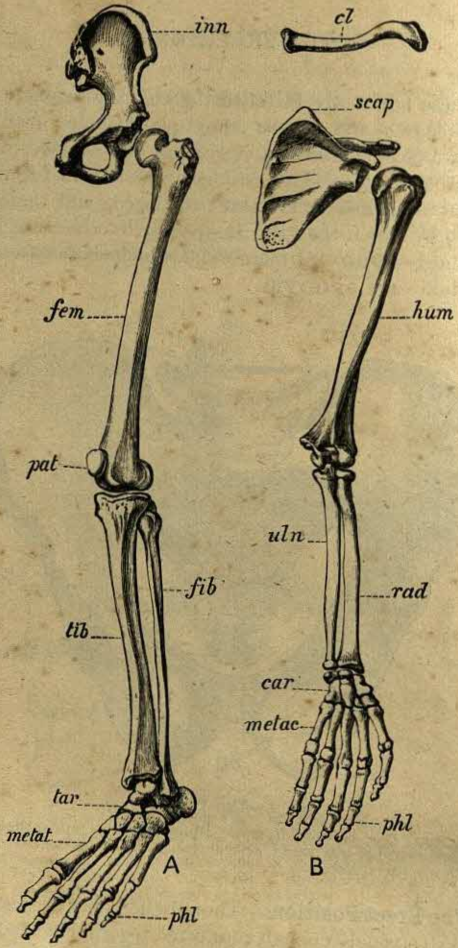

FIG. 5.—THE BONES OF THE LIMBS. FRONT VIEW. LEFT LIMBS.

A, the innominate and bones of the leg; *inn*, innominate; *fem*. femur; *pat*, patella or knee-cap; *tib*, tibia; *fib*, fibula; *tar*, (seven) tarsal bones; *metat*, (five) metatarsal bones; *phl*, (fourteen) phalanges; B, the scapula, clavicle, and bones of the arm; *cl*, clavicle or collar bone; *scap*, scapula or shoulder bone; *hum*, humerus; *rad*, radius; *uln*, ulna; *car*, (eight) carpal bones; *metac*, (five) metacarpal bones; *phl*, (fourteen) phalanges.

oppose and balance one another. Thus, the foot affording the surface of support, the muscles of the calf (Fig. 6, I)

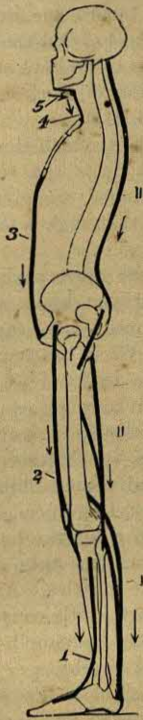

FIG. 6.—A DIAGRAM ILLUSTRATING THE ATTACHMENTS OF SOME OF THE MOST IMPORTANT MUSCLES WHICH KEEP THE BODY IN THE ERECT POSTURE.

I. The muscles of the calf. II. Those of the back of the thigh. III. Those of the spine. These tend to keep the body from falling forward.

1. The muscles of the front of the leg. 2. Those of the front of the thigh. 3. Those of the front of the abdomen. 4, 5. Those of the front of the neck. These tend to keep the body from falling backwards. The arrows indicate the direction of action of the muscles, the foot being fixed.

must contract, or the legs and body would fall forward. But this action tends to bend the leg; and to neutralise this and keep the leg straight, the great muscles in front of the thigh (Fig. 6, 2) must come into play. But these, by the same action, tend to bend the body forward on the legs; and if the body is to be kept straight, they must be neutralised by the action of the muscles of the buttocks and of the back (Fig. 6, III).

The erect position, then, which we assume so easily and without thinking about it, is the result of the combined and accurately proportioned action of a vast number of muscles. What is it that makes them work together in this way?

Let any person in the erect position receive a violent blow on the head, and you know what occurs. On the instant he drops prostrate, in a heap, with his limbs relaxed and powerless. What has happened to him? The blow may have been so inflicted as not to touch a single muscle of the body; it may not cause the loss of a drop of blood; and, indeed, if the "concussion," as it is called, has not been too severe, the sufferer, after a few moments of unconsciousness, will come to himself, and be as well as ever again. Clearly, therefore, no permanent injury has been done to any part of the body, least of all to the muscles, but an influence has been exerted upon a something which governs the muscles. And a similar influence may be the effect of very subtle causes. A strong mental emotion, and even a very bad smell, will, in some people, produce the same effect as a blow.

These observations might lead to the conclusion that it is the mind which directly governs the muscles, but a little further inquiry will show that such is not the case. For people have been so stabbed, or shot in the back, as to cut the spinal cord, without any considerable injury to other parts: and then they have lost the power of standing upright as much as before, though their minds may have remained perfectly clear. And not only have they

lost the power of standing upright under these circumstances, but they no longer retain any power of either feeling what is going on in their legs, or, by an act of their own will, causing motion in them.

And yet, though the mind is thus cut off from the lower limbs, a controlling and governing power over them still remains in the body. For if the soles of the disabled feet be tickled, though the mind does not feel the tickling, the legs will be jerked up, just as would be the case in an uninjured person. Again, if a series of galvanic shocks be sent into the spinal cord, the legs will perform movements even more powerful than those which the will could produce in an uninjured person. And, finally, if the injury is of such a nature as not simply to divide or injure the spinal cord in one place only, but to crush or profoundly disorganise it altogether, all these phenomena cease ; tickling the soles, or sending galvanic shocks along the spine, will produce no effect upon the legs.

By examinations of this kind carried still further, we arrive at the remarkable result that while the brain is the seat of all sensation and mental action, and the primary source of all voluntary muscular contractions, the spinal cord is by itself capable of receiving an impression from the exterior, and converting it not only into a simple muscular contraction, but into a combination of such actions.

Thus, in general terms, we may say of the cerebro-spinal nervous centres, that they have the power, when they receive certain impressions from without, of giving rise to simple or combined muscular contractions.

6. Sensory Organs.—But you will further note that these impressions from without are of very different characters. Any part of the surface of the body may be so affected as to give rise to the sensations of contact, or of heat or cold ; and any or every substance is able, under certain circumstances, to produce these sensations. But only very few and comparatively small portions of the

bodily framework are competent to be affected, in such a manner as to cause the sensations of taste or of smell, of sight or of hearing: and only a few substances, or particular kinds of vibrations, are able so to affect those regions. These very limited parts of the body, which put us in relation with particular kinds of substances, or forms of force, are what are termed **sensory organs**. There are two such organs for sight, two for hearing, two for smell, and one, or more strictly speaking two, for taste.

And now that we have taken this brief view of the structure of the body, of the organs which support it, of the organs which move it, and of the organs which put it in relation with the surrounding world, or, in other words, enable it to move in harmony with influences from without, we must consider the means by which all this wonderful apparatus is kept in working order.

All work, as we have seen, implies waste. The work of the nervous system and that of the muscles, therefore, implies consumption either of their own substance, or of something else. And as the organism can make nothing, it must possess the means of obtaining from without that which it wants, and of throwing off from itself that which it wastes; and we have seen that, in the gross, it does these things. The body feeds, and it excretes. But we must now pass from the broad fact to the mechanism by which the fact is brought about. The organs which convert food into nutriment are the organs of **alimentation**; those which distribute nutriment all over the body are organs of **circulation**; those which get rid of the waste products are organs of **excretion.**

7. **Alimentary Organs.**—The organs of alimentation are the mouth, pharynx, gullet, stomach, and intestines, with their appendages. What they do is, first to receive and grind the food. They then act upon it with chemical agents, of which they possess a store which is renewed as fast as it is used; and in this way convert the food by processes of digestion into a fluid containing nutritious

matters in solution or suspension, and innutritious dregs or fæces.

8. **Circulatory Organs.**—A system of minute tubes, with very thin walls, termed **capillaries**, is distributed through the whole organism except the epidermis and its products, the epithelium, the cartilages, and the substance of the teeth. On all sides, these tubes pass into others, which are called **arteries** and **veins**; while these, becoming larger and larger, at length open into the **heart**, an organ which, as we have seen, is placed in the thorax. During life, these tubes and the chambers of the heart, with which they are connected, are all full of liquid, which is, for the most part, that red fluid with which we are all familiar as **blood**.

The walls of the heart are muscular, and contract rhythmically, or at regular intervals. By means of these contractions the blood which its cavities contain is driven in jets out of these cavities, into the arteries, and thence into the capillaries, whence it returns by the veins back into the heart.

This is the **circulation of the blood**.

Now the fluid containing the dissolved nutritive matters which are the result of the process of digestion, traverses the very thin layer of soft and permeable tissue which separates the cavity of the alimentary canal from the cavities of the innumerable capillary vessels which lie in the walls of that canal, and so enters the blood, with which those capillaries are filled. Whirled away by the torrent of the circulation, the blood, thus charged with nutritive matter, enters the heart, and is thence propelled into the organs of the body. To these organs it supplies the nutriment with which it is charged; from them it takes their waste products, and, finally, returns by the veins to the heart, loaded with useless and injurious excretions, which sooner or later take the form of water, carbonic acid, and urea.

9. **Excretory Organs.**—These excretionary matters

are separated from the blood by the **excretory organs**, of which there are three—the **skin**, the **lungs**, and the **kidneys**.

Different as these organs may be in appearance, they are constructed upon one and the same principle. Each, in ultimate analysis, consists of a very thin sheet of tissue, like so much delicate blotting-paper, the one face of which is free, or lines a cavity in communication with the exterior of the body, while the other is in contact with the blood which has to be purified.

The excreted matters are, as it were (though, as we shall see, in a peculiar way), strained from the blood, through this delicate layer of tissue, and on to its free surface, whence they make their escape.

Each of these organs is especially concerned in the elimination of one of the chief waste products—water, carbonic acid, and urea—though it may at the same time be a means of escape for the others. Thus the lungs are especially busied in getting rid of carbonic acid, but at the same time they give off a good deal of water. The duty of the kidneys is to excrete urea (together with other substances, chiefly salts), but at the same time they pass away a large quantity of water and a trifling amount of carbonic acid; while the skin gives off much water, some amount of carbonic acid, and a certain quantity of saline matter, among which a trace of urea may be, sometimes, though very doubtfully, present.

10. **Respiratory Organs.**—Finally the lungs play a double part, being not merely eliminators of waste, or excretionary products, but importers into the economy of a substance which is not exactly either food or drink, but something as important as either,—to wit, **oxygen**.

As the carbonic acid (and water) is passing from the blood through the lungs into the external air, oxygen is passing from the air through the lungs into the blood, and is carried, as we shall see, by the blood to all parts of the body. We have seen (p. 6) that the waste which

leaves the body contains more oxygen than the food which enters the body. Indeed oxidation, the oxygen being supplied by the blood, is going on all over the body. All parts of the body are thus continually being oxidised, or, in other words, are continually burning, some more rapidly and fiercely than others. And this burning, though it is carried on in a peculiar manner, so as never to give rise to a flame, yet nevertheless produces an amount of heat which is as efficient as a fire to raise the blood to a temperature of about 37° C. (98·6° F.); and this hot fluid, incessantly renewed in all parts of the economy by the torrent of the circulation, warms the body, as a house is warmed by a hot-water apparatus. Nor is it alone the heat of the body which is provided by this oxidation; the energy which appears in the muscular work done by the body has the same source. Just as the burning of the coal in a steam-engine supplies the motive power which drives the wheels, so, though in a peculiar way, the oxidation of the muscles (and thus ultimately of the food) supplies the motive power of those muscular contractions which carry out the movements of the body. The food, like coal combustible or capable of oxidation, is built up into the living body, which in like manner combustible, is continually being oxidised by the oxygen from the blood, thus doing work and giving out heat. Some of the food perhaps may be oxidised without ever actually forming part of the body or after it has already become waste matter, but this does not concern us now.

11. **Coordinating Action of the Nervous System.**—These alimentary, circulatory or distributive, excretory, and respiratory (oxidational) processes would however be worse than useless if they were not kept in strict proportion one to another. If the state of physiological balance is to be maintained, not only must the quantity of aliment taken be at least equivalent to the quantity of matter excreted; but that aliment must be distributed with due

rapidity to the seat of each local waste. The circulatory system is the commissariat of the physiological army.

Again, if the body is to be maintained at a tolerably even temperature, while that of the air is constantly varying, the condition of the hot-water apparatus must be most carefully regulated.

In other words, a **coordinating organ** must be added to the organs already mentioned, and this is found in the **nervous system**, which not only possesses the function already described of enabling us to move our bodies and to know what is going on in the external world; but makes us aware of the need of food, enables us to discriminate nutritious from innutritious matters, and to exert the muscular actions needful for seizing, killing, and cooking; guides the hand to the mouth, governs all the movements of the jaws and of the alimentary canal, and determines the due supply of the juices necessary for digestion. By it, the working of the heart can be properly adjusted and the calibres of the distributing pipes can be regulated, so as indirectly to govern the excretory and oxidational processes, which are also additionally and more directly affected by other actions of the nervous system.

The nervous system has often been compared to a telephone system with its exchange (the brain and spinal cord) and its wires (the fibres) which go to and fro in communication with the various instruments in which the messages are given or heard (sensory or motor nerve endings). In addition to this system there is another coordinating system which may be compared to a wireless system of communication. The messages do not run along fibres but are chemical substances which are produced in one organ of the body and carried by the blood to another organ, perhaps in some very remote part. They throw the particular organ for which they are destined into activity without affecting other parts of the body. Such messengers are called **hormones**.

12. Life and Death.—The various functions which

have been thus briefly indicated constitute the greater part of what are called the *vital actions* of the human body, and so long as they are performed, the body is said to possess *life*. The cessation of the performance of these functions is what is ordinarily called *death*.

But there are really several kinds of death, which may, in the first place, be distinguished from one another under the two heads of *local* and of *general* death.

(i) **Local death** is going on at every moment, and in most, if not in all, parts of the living body. Individual cells of the epidermis and of the epithelium are incessantly dying and being cast off, to be replaced by others which are, as constantly, coming into separate existence. The like is true of blood-corpuscles, and probably of many other elements of the tissues.

This form of local death is insensible to ourselves, and is essential to the due maintenance of life. But, occasionally, local death occurs on a larger scale, as the result of injury, or as the consequence of disease. A burn, for example, may suddenly kill more or less of the skin; or part of the tissues of the skin may die, as in the case of the slough which lies in the midst of a boil; or a whole limb may die, and exhibit the strange phenomena of *mortification*.

The local death of some tissues is followed by their regeneration. Not only all the forms of epidermis and epithelium, but nerves, connective tissue, bone, and at any rate, some muscles, may be thus reproduced, even on a large scale.

(ii) **General death** is of two kinds, *death of the body as a whole*, and *death of the tissues*. By the former term is implied the absolute cessation of the functions of the brain, of the circulatory, and of the respiratory organs; by the latter, the entire disappearance of the vital actions of the ultimate structural constituents of the body. When death takes place, the body, as a whole, dies first, the death of the tissues not occurring until after an interval, which is sometimes considerable.

Hence it is that, for a while after what is ordinarily called death, the muscles of an executed criminal may be made to contract by the application of proper stimuli, and the heart may even be excised and made to beat for a considerable time.. The muscles are not dead, though the man is.

13. **Modes of Death.**—The modes in which death is brought about appear at first sight to be extremely varied. We speak of natural death by old age, or by some of the endless forms of disease; of violent death by starvation, or by the innumerable varieties of injury, or poison. But, in reality, the immediate cause of death is always the stoppage of the functions of one of three organs; the cerebro-spinal nervous system, the lungs, or the heart. Thus, a man may be instantly killed by such an injury to a part of the brain which is called the **spinal bulb** or **medulla oblongata** (see Lesson XI.) as may be produced by hanging, or breaking the neck.

Or death may be the immediate result of suffocation by strangulation, smothering, or drowning,—or, in other words, of stoppage of the respiratory functions.

Or, finally, death ensues at once when the heart ceases to propel blood. These three organs—the brain, the lungs, and the heart—have been fancifully termed the *tripod of life*.

In ultimate analysis, however, life has but two legs to stand upon, the lungs and the heart, for death through the brain is always the effect of the secondary action of the injury to that organ upon the lungs or the heart. The functions of the brain cease, when either respiration or circulation is at an end. But if circulation and respiration are kept up artificially, the brain may be removed without causing death. On the other hand, if the blood be not aërated, its circulation by the heart cannot preserve life; and, if the circulation be at an end, mere aëration of the blood in the lungs is equally ineffectual for the prevention of death.

With the cessation of life, the everyday forces of the inorganic world no longer remain the servants of the

bodily frame, as they were during life, but become its masters. Oxygen, the slave of the living organism, becomes the lord of the dead body. Atom by atom, the complex molecules of the tissues are taken to pieces and reduced to simpler and more oxidised substances, until the soft parts are dissipated chiefly in the form of carbonic acid, ammonia, water, and soluble salts, and the bones and teeth alone remain. But not even these dense and earthy structures are competent to offer a permanent resistance to water and air. Sooner or later the animal basis which holds together the earthy salts decomposes and dissolves—the solid structures become friable, and break down into powder. Finally, they dissolve and are diffused among the waters of the surface of the globe, just as the gaseous products of decomposition are dissipated through its atmosphere.

It is impossible to follow, with any degree of certainty, wanderings more varied and more extensive than those imagined by the ancient sages who held the doctrine of transmigration; but the chances are, that sooner or later, some, if not all, of the scattered atoms will be gathered into new forms of life.

The sun's rays, acting through the vegetable world, build up some of the wandering molecules of carbonic acid, of water, of ammonia, and of salts, into the fabric of plants. The plants are devoured by animals, animals devour one another, man devours both plants and other animals; and hence it is very possible that atoms which once formed an integral part of the busy brain of Julius Cæsar may now enter into the composition of Cæsar the negro in Alabama, and of Cæsar the house-dog in an English homestead.

And thus there is sober truth in the words which Shakespeare puts into the mouth of Hamlet—

> "Imperial Cæsar, dead and turned to clay,
> Might stop a hole to keep the wind away;
> Oh that that earth, which kept the world in awe,
> Should patch a wall, to expel the winter's flaw!"

LESSON II

THE ORGANS OF CIRCULATION

Part I.—The Blood Vascular System and the Circulation

1. The Capillaries.—Almost all parts of the body are *vascular*; that is to say, they are traversed by minute and very close-set canals, which open into one another so as to constitute a small-meshed network, and confer upon these parts a spongy texture. The canals, or rather tubes, are provided with distinct but very delicate walls, composed of what at first sight appears to be a structureless membrane,

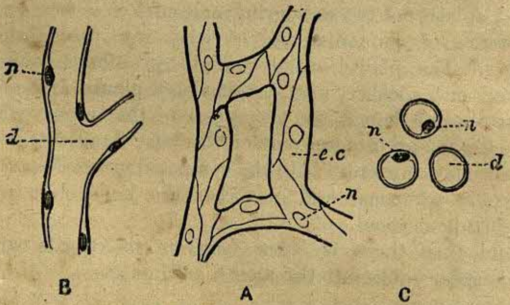

Fig. 7.—Capillaries.

A, surface view; B, cut lengthwise; C, cut across; *e c*, endothelial cells; *n*, nuclei; *d*, the lumen or bore.

but is in reality formed of a number of thin scales, called "cells," cemented together at their edges (Fig. 7, A, *e.c*); in each of these cells lies a small oval body (Fig. 7, *n*), termed a **nucleus.**

These tubes are the **blood capillaries.** They vary in diameter from 14 μ to 16 μ ($\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch)[1]; they are sometimes disposed in loops, sometimes in long, sometimes in wide, sometimes in narrow meshes; and the diameters of these meshes, or, in other words, the interspaces between the capillaries, are sometimes hardly wider than the diameter of a capillary, sometimes many times as wide (see Figs. 25, 39, 58, and 64). These interspaces are occupied by the substance of the tissue which the capillaries permeate, so that the ultimate anatomical components of every part of the body are, strictly speaking, outside the vessels, or *extra-vascular.*

But there are certain parts of the body in which these blood-capillaries are absent. These are the epidermis and epithelium, the nails and hairs, the substance of the teeth, and to a certain extent the cartilages and the transparent coat (cornea) of the eye in front; which may and do attain a very considerable thickness or length, and yet contain no blood-vessels. However, since we have seen that all the tissues are really extra-vascular, these differ only in degree from the rest. The circumstance that all the tissues are outside the vessels by no means interferes with their being bathed by the fluid which is inside the vessels. In fact, the walls of the capillaries are so exceedingly thin that their fluid contents readily exude through the delicate membrane of which they are composed, and irrigate the tissues in which they lie.

2. **The Arteries and Veins.**—The capillary tubes so far described contain, during life, the red fluid, **blood,** and are continued on opposite sides, into somewhat larger

[1] The ordinarily used unit of histological measurement is $\frac{1}{1000}$ of a millimeter, and is usually represented by the Greek letter μ, which stands for micro-millimeter. Since one millimeter is very nearly $\frac{1}{25}$ of an inch $\mu = \frac{1}{25000}$ of an inch.

tubes, with thicker walls, which are the smallest **arteries**, on the one side and **veins** on the other, and these again join on to larger arteries and veins, which ultimately communicate by a few principal arterial and venous trunks with the heart.

The mere fact that the walls of these vessels are thicker than those of the capillaries constitutes an important difference between the capillaries and the small arteries and veins; for the walls of the latter are thus rendered far less permeable to fluids, and that thorough irrigation of the tissues, which is effected by the capillaries, cannot be performed by them.

The most important difference between these vessels and the capillaries, however, lies in the circumstance that their walls are not only thicker, but also more complex, being composed of several coats, one, at least, of which is muscular. The number, arrangement, and even nature of these coats differ according to the size of the vessels, and are not the same in the veins as in the arteries, though the smallest veins and arteries tend to resemble each other.

(i) **The Structure of an Artery.**—If we take one of the smallest arteries, we find, first, a very delicate lining of cells constituting a sort of epithelium continuous with the cells which form the entire thickness of the wall of the capillaries. Outside this comes the muscular coat, consisting of a thin layer of muscle-fibres of the kind called plain or non-striated (see Lesson VII.), made up of flattened spindle-shaped cells with an elongated nucleus, wrapped round the vessel at right angles to its length. Outside this muscular coat is a thin layer of fibrous connective tissue intermixed with a variable amount of fibres of elastic tissue (see Lesson XII.). The walls of the smallest arteries are thus seen to be made up essentially of three layers; the inner cellular, the middle muscular, the outer of connective tissue. The larger arteries are similarly composed of three layers or coats, which are, however, thicker and

more complex in structure. The inner coat now consists of thin flattened cells lying on a distinct and special layer of elastic tissue of variable thickness. The middle coat, to which the thickness of the arterial wall is chiefly due, consists of alternating layers of plain muscle fibres, lying transversely to the axis of the vessel, and of elastic fibres which as a rule run lengthwise. The outer coat, also of considerable thickness, is made up of fibrous connective tissue, mixed with fibres of elastic tissue.

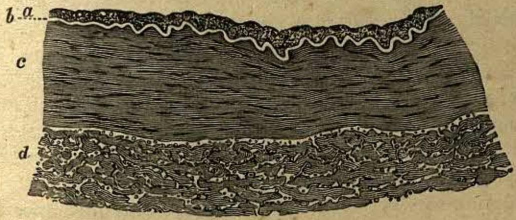

FIG. 8.—TRANSVERSE SECTION OF PART OF THE WALL OF A MEDIUM-SIZED ARTERY, MAGNIFIED 75 DIAMETERS. (SCHÄFER.)

a, epithelial (endothelial) layer of inner coat; *b*, elastic layer (fenestrated membrane) of inner coat, appearing in section as a bright line; *c*, muscular layers (middle coat); *d*, outer coat, consisting of connective tissue bundles, interspersed with connective tissue nuclei, and, especially near the muscular coat, with elastic fibres cut across.

From the above description of the structure of an artery we see at once that arteries are **strong, muscular** and **elastic.** The largest arteries are, as a rule, characteristically more elastic than the smaller, while in the latter the muscular tissue is present in large amount *relatively* to the elastic tissue. The significance of this difference will become apparent later on (see pp. 62 and 65).

The plain muscular fibres in the arterial wall possess that same power of contraction, or shortening in the long, and broadening in the narrow, directions, which, as was stated in the preceding Lesson, is the special property of muscular tissue. And when they exercise this power, they,

of course, narrow the calibre of the vessel, just as squeezing it with the hand or in any other way would do; and this contraction may go so far as, in some cases, to reduce the cavity of the vessel almost to nothing, and to render it practically impervious.

The state of contraction of these muscles of the small arteries is regulated, like that of other muscles, by their nerves; or, in other words, the nerves supplied to the vessels determine whether the passage through these tubes should be wide and free, or narrow and obstructed. Thus while the small arteries lose the function, which the capillaries possess, of directly irrigating the tissues by transudation, they gain that of **regulating the supply** of fluid to the irrigators or capillaries themselves. The contraction, or dilation, of the arteries which supply a set of capillaries, comes to the same result as lowering or raising the sluice-gates of a system of irrigation-canals. Thus the one great and all-important use of the muscular tissue of the smaller arteries is *to determine and control the supply of blood to each part of the body, according to the varying needs of that part.*

The smaller arteries and veins severally unite into, or are branches of, larger arterial or venous trunks, which again spring from or unite into still larger ones, and these, at length, communicate by a few principal arterial and venous trunks with the heart.

(ii) **The Structure of a Vein.**—The wall of a vein is structurally similar to that of an artery in so far that it consists essentially of the same three layers or coats, but the distinction between the middle and outer coats, so easily made out in an artery, is usually very obscure in a vein or even altogether wanting in some veins. It differs from that of an artery chiefly in the fact that it is thinner, less muscular and less elastic, and contains *relatively* more connective tissue. Hence the walls of a vein collapse or fall together when the vessel is empty, whereas those of an artery do not.

This is one great difference between the arteries and the veins; the other is the presence of what are termed **valves** in a great many of the veins, especially in those which lie in muscular parts of the body. They are absent in the largest trunks such as the superior and inferior vena cava, and in the smallest branches, as also in the portal, pulmonary, and cerebral veins, and in those of the bones.

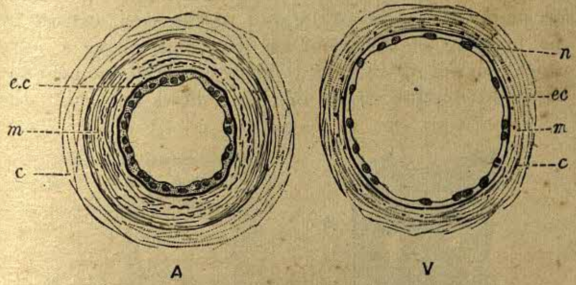

FIG. 9.—TRANSVERSE SECTION OF AN ARTERY AND OF A CORRESPONDING VEIN.

A, artery; V, vein; *ec*, endothelial cells; *m*, muscular (middle) coat; *c*, connective tissue (outer) coat; *n*, nuclei of endothelial cells.

These valves are pouch-like folds of the inner wall of the vein. The bottom of the pouch is turned towards those capillaries from which the vein springs. The free edge of the pouch is directed the other way, or towards the heart. The action of these pouches is to impede the passage of any fluid from the heart towards the capillaries, while they do not interfere with fluid passing in the opposite direction (Fig. 10). The working of some of these valves may be very easily demonstrated in the living body. When the arm is bared, blue veins may be seen running from the hand, under the skin, to the upper arm. The diameter of these veins is pretty even, and diminishes

regularly towards the hand, so long as the current of the blood, which is running in them, from the hand to the upper arm, is uninterrupted.

But if a finger be pressed upon the upper part of one of these veins, and then passed downwards along it, so as to drive the blood which it contains backwards, sundry swellings, like little knots, will suddenly make their appearance at several points in the length of the vein, where nothing of the kind was visible before. These swellings are simply dilatations of the wall of the vein, caused by the pressure of the blood on that wall, above a valve which opposes its backward progress. The moment the backward impulse ceases the blood flows on again; the

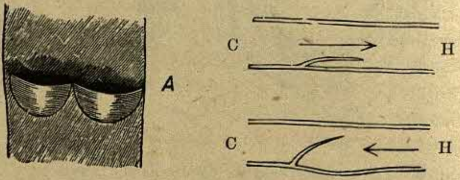

FIG. 10.—THE VALVES OF VEINS.

C, H, C, H, diagrammatic sections of veins with valves. In the upper figure the blood is supposed to be flowing in the direction of the arrow, towards the heart; in the lower, back towards the capillaries; C, capillary side; H, heart side. A, a vein laid open to show a pair of pouch-shaped valves.

valve, swinging back towards the wall of the vein, affords no obstacle to its progress, and the distention caused by its pressure disappears (Fig. 10).

These valves play an important part in determining the flow of blood along the veins from the capillaries towards the heart. This they do *not* in virtue of any propulsive power of their own, *but in response to pressure applied to the veins from their exterior*. Such pressure tends to squeeze the blood out of that part of the vein on which it is brought to bear; but since the valves only open towards the heart the blood is thereby driven on in the

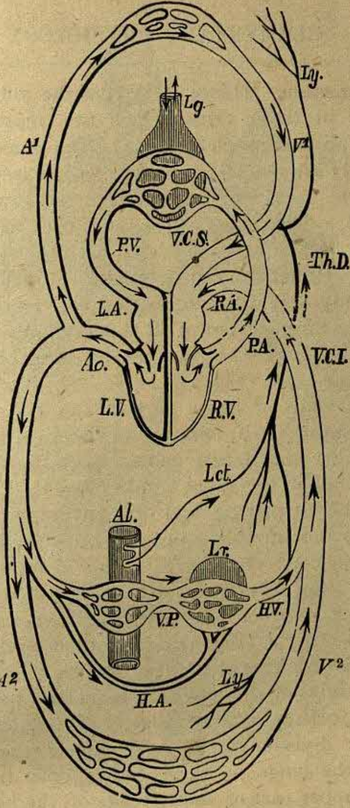

FIG. 11.—DIAGRAM OF THE HEART AND VESSELS, WITH THE COURSE OF THE CIRCULATION, VIEWED FROM BEHIND, SO THAT THE PROPER LEFT OF THE OBSERVER CORRESPONDS WITH THE LEFT SIDE OF THE HEART IN THE DIAGRAM.

L.A. left auricle; *L.V.* left ventricle; *Ao.* aorta; A^1. arteries to the upper part of the body; A^2. arteries to the lower part of the body; *H.A.* hepatic artery, which supplies the liver with part of its blood; V^1. veins of the upper part of the body; V^2. veins of the lower part of the body; *V.P.* vena portæ; *H.V.* hepatic vein; *V.C.I.* inferior vena cava; *V.C.S.* superior vena cava; *R.A.* right auricle; *R.V.* right ventricle; *P.A.* pulmonary artery; *Lg.* lung; *P.V.* pulmonary vein; *Lct.* lacteals; *Ly.* lymphatics; *Th.D.* thoracic duct; *Al.* alimentary canal; *Lr.* liver. The arrows indicate the course of the blood, lymph, and chyle. The vessels which contain arterial blood have dark contours, while those which carry venous blood have light contours.

desired direction. Hence it is that the valves are most numerous in those veins which are most subject to muscular pressure, such as those of the arms and legs.

The only arteries which possess valves are the primary trunks—the aorta and pulmonary artery—which spring from the heart, but these valves, since they really belong to the heart, will be best considered with that organ.

3. The General Arrangement of Blood-vessels in the Body.—It will now be desirable to take a general view of the arrangement of all these different vessels, and of their relations to the great central organ of the vascular system—the heart (Fig. 11).

All the veins of every part of the body, except the lungs, the heart itself, and certain viscera of the abdomen, join together into larger veins, which, sooner or later, open into one of two great trunks (Fig. 11, *V.C.S. V.C.I.*) termed the **superior** and the **inferior vena cava**, which debouch into the upper or broad end of the right half of the heart.

All the arteries of every part of the body, except the lungs, are more or less remote branches of one great trunk—the **aorta** (Fig. 11, *Ao.*), which springs from the lower division of the left half of the heart.

The arteries of the lungs are branches of a great trunk, the **pulmonary artery** (Fig. 11, *P.A.*), springing from the lower division of the right side of the heart. The veins of the lungs, on the contrary, open by four trunks into the upper part of the left side of the heart (Fig. 11, *P.V.*), by the **pulmonary veins.**

Thus the venous trunks open into the upper division of each half of the heart: those of the body in general into that of the right half, those of the lungs into that of the left half; while the arterial trunks spring from the lower moieties of each half of the heart: that for the body in general from the left side, and that for the lungs from the right side.

Hence it follows that the great artery of the body, and

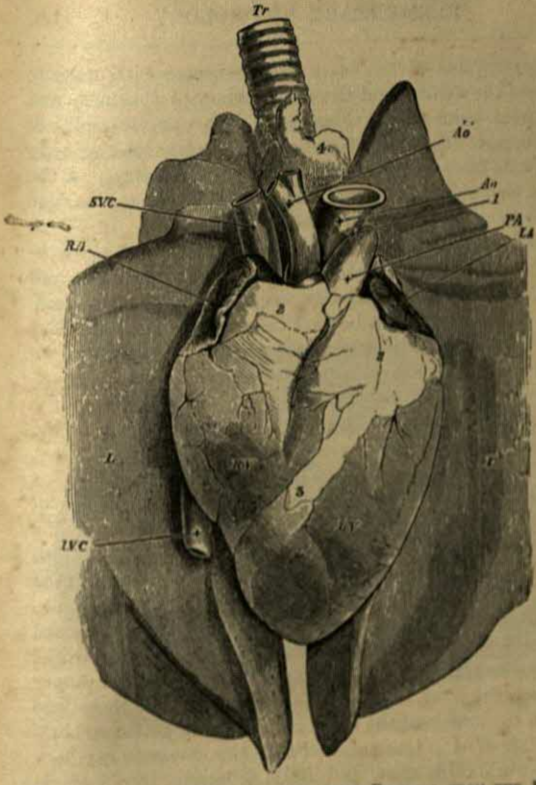

FIG. 12.—HEART OF SHEEP, AS SEEN AFTER REMOVAL FROM THE BODY, LYING UPON THE TWO LUNGS. THE PERICARDIUM HAS BEEN CUT AWAY, BUT NO OTHER DISSECTION MADE.

R.A. auricular appendage of right auricle; *L.A.* auricular appendage of left auricle; *R.V.* right ventricle; *L.V.* left ventricle; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; *P.A.* pulmonary artery; *Ao*, aorta; *A'o'*, innominate branch from aorta dividing into subclavian and carotid arteries; *L*, lung; *Tr.* trachea. 1, solid cord often present, the remnant of a once open communication between the pulmonary artery and aorta. 2, masses of fat at the bases of the ventricle hiding from view the greater part of the auricles. 3, line of fat marking the division between the two ventricles. 4, mass of fat covering end of trachea.

the great veins of the body, are connected with opposite sides of the heart; and the great artery of the lungs and the great veins of the lungs also with opposite sides of that organ. On the other hand, the veins of the body open into the same side of the heart as the artery of the lungs, and the veins of the lungs open into the same side of the heart as the artery of the body.

The arteries which open into the capillaries of the substance of the heart are called **coronary arteries**, and arise, like the other arteries, from the aorta, but quite close to its origin, just beyond the semilunar valves. But the **coronary vein**, which is formed by the union of the small veins which arise from the capillaries of the heart, does not open into either of the venæ cavæ, but pours the blood which it contains directly into the division of the heart into which these venæ cavæ open—that is to say, into the right upper division (Fig. 19, *b*).

The abdominal viscera referred to above, the veins of which do not take the usual course, are the stomach, the intestines, the spleen, and the pancreas. These veins all combine into a single trunk, which is termed the **portal vein** (Fig. 11, *V.P.*), but this trunk does not open into the inferior vena cava. On the contrary, having reached the liver, it enters the substance of that organ, and breaks up into an immense multitude of capillaries, which ramify through the liver, and become connected with those into which the artery of the liver, called the **hepatic artery** (Fig. 11, *H.A.*), branches. From this common capillary mesh-work veins arise, and unite, at length, into a single trunk, the **hepatic vein** (Fig. 11, *H.V.*), which emerges from the liver, and opens into the **inferior vena cava.** The flow of blood from the abdominal viscera through the liver to the hepatic vein is called the **portal circulation.** The portal vein is the only great vein in the body which branches out and becomes continuous with the capillaries of an organ, like an artery. But certain small veins in the kidney are similarly arranged. (Lesson V.)

The *shortest possible course* which any particle of the blood can take in order to pass from one side of the heart to the other, is to leave the aorta by one of the coronary arteries, and return to the right auricle by the coronary vein. And in order to pass through the *greatest possible number of capillaries* and return to the point from which it started, a particle of blood must leave the heart by the aorta and traverse the arteries which supply the alimentary canal, spleen or pancreas. It then enteres 1stly, the capillaries of one of these organs; 2ndly, the capillaries

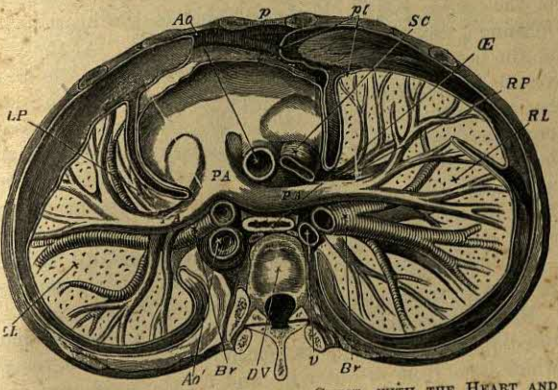

FIG. 13.—TRANSVERSE SECTION OF THE CHEST, WITH THE HEART AND LUNGS IN PLACE. (A little diagrammatic.)

D.V. dorsal vertebra, or joint of the backbone; *Ao*, *Ao'*. aorta, the top of its arch being cut away in this section; *S.C.* superior vena cava; *P.A.* pulmonary artery, divided into a branch for each lung; *L.P.* *R.P.* left and right pulmonary veins; *Br.* bronchi; *R.L.* *L.L.* right and left lungs; *Œ.* the gullet or œsophagus; *p.* outer bag of pericardium; *pl.* the two layers of pleura; *v.* azygos vein.

of the liver; and, 3rdly, after passing through the right side of the heart, the capillaries of the lungs, from which it returns to the left side and eventually to the aorta.

4. The Heart.—The heart (Figs. 12 and 14), to which all the vessels in the body have now been directly or

indirectly traced, is an organ, the size of which is usually roughly estimated as equal to that of the closed fist of the person to whom it belongs, and which has a broad end turned upwards and backwards, and rather to the right side, called its **base** : and a pointed end which is called its **apex**, turned downwards and forwards, and to the left side, so as to lie opposite the interval between the fifth and sixth ribs.

It is lodged between the lungs, nearer the front than the back wall of the chest, and is enclosed in a sort of double bag—the **pericardium** (Fig. 13, *p.*). One-half of the double bag is closely adherent to the heart itself, forming a thin coat upon its outer surface. At the base of the heart, this half of the bag passes on to the great vessels which spring from, or open into, that organ ; and becomes continuous with the other half, which loosely envelopes both the heart and the adherent half of the bag. Between the two layers of the pericardium, consequently, there is a completely closed, narrow cavity, lined by an epithelium, and containing in its interior a small quantity of clear fluid, the **pericardial fluid.**[1] The outer layer of the pericardium is firmly connected below with the upper surface of the diaphragm.

But the heart cannot be said to depend altogether upon the diaphragm for support, inasmuch as the great vessels which issue from or enter it—and for the most part pass upwards from its base—help to suspend and keep it in place.

Thus the heart is coated, outside, by one layer of the pericardium. Inside, it contains two great cavities or "divisions," as they have been termed above, completely separated by a fixed partition which extends from the base to the apex of the heart ; and consequently, having

[1] This fluid, like that contained in the peritoneum, pleura, and other shut sacs of a similar character to the pericardium, used to be called *serum*; whence the membranes forming the walls of these sacs are frequently termed *serous membranes*. The fluid is, however, in reality a form of lymph. (See Lesson III.)

no direct communication with one another. Each of these two great cavities is further subdivided, not longitudinally but transversely, by a movable partition. The cavity above the transverse partition on each side is called the **auricle**; the cavity below, the **ventricle**—right or left as the case may be.

Each of the four cavities has the same capacity, and is capable of containing from 4 to 6 cubic inches of water

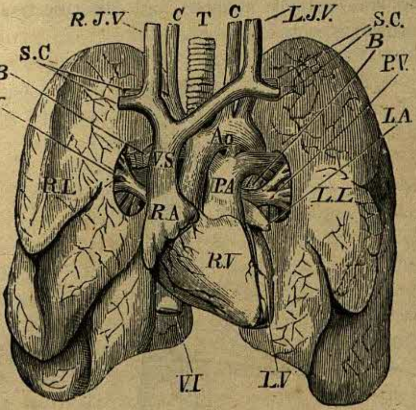

FIG. 14.—THE HEART, GREAT VESSELS, AND LUNGS. (FRONT VIEW.)

R.V. right ventricle; *L.V.* left ventricle; *R.A.* right auricle; *L.A.* left auricle; *Ao.* aorta; *P.A.* pulmonary artery; *P.V.* pulmonary veins; *R.L.* right lung; *L.L.* left lung; *V.S.* vena cava superior; *S.C.* subclavian vessels; *C.* carotids; *R.J.V.* and *L.J.V* right and left jugular veins; *V.I.* vena cava inferior; *T.* trachea; *B.* bronchi.

All the great vessels but those of the lungs are cut.

(70 to 100 cubic centimeters). The walls of the auricles are much thinner than those of the ventricles. The wall of the left ventricle is much thicker than that of the right ventricle; but no such difference is perceptible between the two auricles (Figs. 16 and 17, 1 and 3).

In fact, as we shall see, the ventricles have more work to do than the auricles, and the left ventricle more to do than the right. Hence the ventricles have more muscular substance than the auricles, and the left ventricle than the right; and it is this excess of muscular substance which gives rise to the excess of thickness observed in the left ventricle.

The muscular fibres of the heart are of a peculiar nature, resembling those of the chief muscles of the body in being transversely striated, but differing from them in many other respects.

FIG. 15.—CARDIAC FIBRE CELLS.

Two cells isolated from the heart. *n*, nucleus; *l*, line of junction between the two cells; *p*, process joining a similar process of another cell. (Magnified 400 diameters.)

Cardiac Muscular Tissue.—The muscular tissue of the heart is intermediate in character between striated and non-striated muscle. Like the non-striated muscle, it is composed of cells, each containing a single nucleus, and possessing no sarcolemma. But the cells (Fig. 15) are generally short and broad, frequently branched or irregular in shape, and their substance is more or less distinctly

striated, like the substance of a striated fibre. A number of such cells are joined by cement substance into sets of anastomosing fibres, which are built up in a complex interwoven manner into the walls of the ventricles and auricles.

The cavities of the heart are lined by a smooth, shiny membrane called the **endocardium**, which consists of a layer of connective tissue covered with thin flattened cells continuous with and similar to those which form the wall of the capillaries and which line the arteries and veins. At the junction between the auricles and ventricles, the apertures of communication between their cavities, called the **auriculo-ventricular apertures**, are strengthened by **fibrous rings** of connective tissue. To these rings the movable partitions, or valves, between the auricles and ventricles, the arrangement of which must next be considered, are attached.

5. The Valves of the Heart.—There are three of these partitions attached to the circumference of the right auriculo-ventricular aperture, and two to that of the left (Figs. 16, 17, 18, 19, *t v*, *m v*). Each is a broad, thin, but very tough and strong triangular fold of connective tissue (see Lesson XII.) covered by endocardium, attached by its base, which joins on to its fellow, to the auriculo-ventricular fibrous ring, and hanging with its point downwards into the ventricular cavity. On the right side there are, therefore, three of these broad, pointed membranes, whence the whole apparatus is called the **tricuspid valve**. On the left side, there are but two, which, when detached from all their connexions but the auriculo-ventricular ring, look something like a bishop's mitre, and hence bear the name of the **mitral valve**.

The edges and apices of the valves are not completely free and loose. On the contrary, a number of fine, but strong, tendinous cords, called **chordæ tendineæ**, connect them with some column-like elevations of the fleshy substance of the walls of the ventricle, which are termed

papillary muscles (Figs. 16 and 17, *pp*); similar column-like elevations of the walls of the ventricles, but

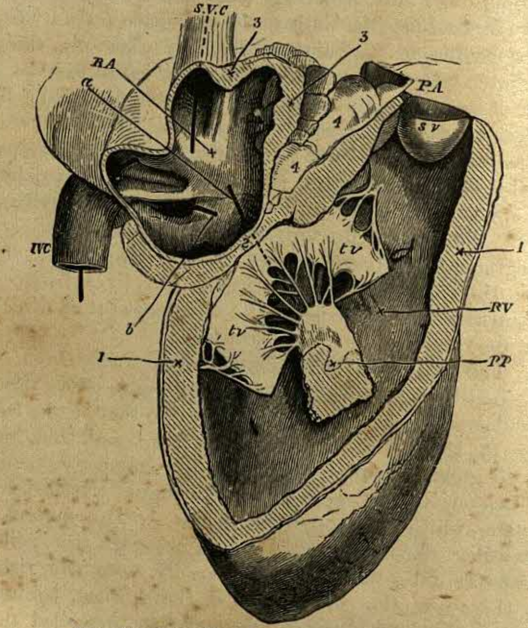

FIG. 16.—RIGHT SIDE OF THE HEART OF A SHEEP.

R.A. cavity of right auricle; *S.V.C.* superior vena cava; *I.V.C.* inferior vena cava; (a style has been passed through each of these;) *a*, a style passed from the auricle to the ventricle through the auriculo-ventricular orifice; *b*, a style passed into the coronary vein.

R.V. cavity of right ventricle; *tv*, *tv*, two flaps of the tricuspid valve; the third is dimly seen behind them, the style *a* passing between the three. Between the two flaps, and attached to them by *chordæ tendineæ*, is seen a papillary muscle, *pp*, cut away from its attachment to that portion of the wall of the ventricle which has been removed. Above, the ventricle terminates somewhat like a funnel in the pulmonary artery, *P.A.* One of the pockets of the semilunar valve *sv*, is seen in its entirety, another partially.

1, the wall of the ventricle cut across; 2, the position of the auriculo-ventricular ring; 3, the wall of the auricle; 4, masses of fat lodged between the auricle and pulmonary artery.

having no chordæ tendineæ attached to them, are called **columnæ carneæ**.

It follows, from this arrangement, that the valves oppose no obstacle to the passage of fluid from the auricles to the ventricles; but if any should be forced the other way, it will at once get between the valve and the wall of the heart, and drive the valve backwards and upwards. Partly because they soon meet in the middle and oppose one another's action, and partly because the *chordæ tendineæ* hold their edges and prevent them from going back too far, the valves, thus forced back, give rise to the formation of a complete transverse partition between the ventricle and the auricle, through which no fluid can pass.

Where the aorta opens into the left ventricle, and where the pulmonary artery opens into the right ventricle another valvular apparatus is placed, consisting in each case of three pouch-like valves called the **semilunar valves** (Fig. 16, *s.v.*; Figs. 18 and 19, *Ao. P.A.*), which are similar to those of the veins. Since they are placed on the same level and meet in the middle line, they completely stop the passage when any fluid is forced along the artery towards the heart. On the other hand, these valves flap back and allow any fluid to pass from the heart into the artery, with the utmost readiness.

The action of the auriculo-ventricular valves may be demonstrated with great ease on a sheep's heart, in which the aorta and pulmonary artery have been tied and the greater part of the auricles cut away, by pouring water into the ventricles through the auriculo-ventricular aperture. The tricuspid and mitral valves then usually become closed by the upward pressure of the water which gets behind them. Or, if the ventricles be nearly filled, the valves may be made to come together at once by gently squeezing the ventricles. In like manner, if the base of the aorta, or pulmonary artery, be cut out of the heart, so as not to injure the semilunar valves, water

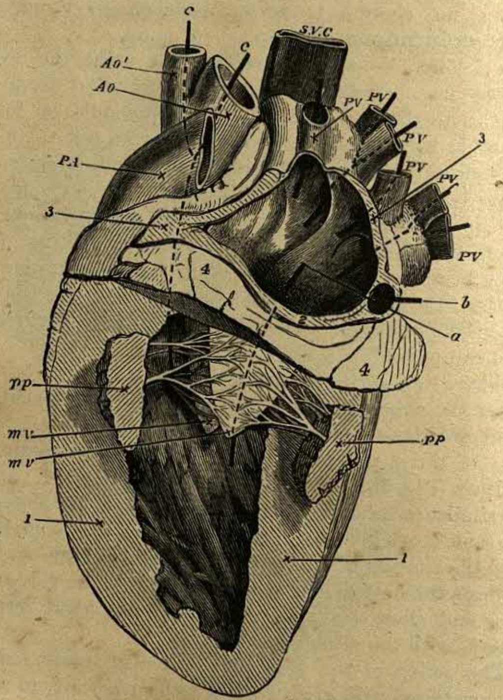

FIG. 17.—LEFT SIDE OF THE HEART OF A SHEEP (LAID OPEN).

P.V. pulmonary veins opening into the left auricle by four openings, as shown by the styles; *a*, a style passed from auricle into ventricle through the auriculo-ventricular orifice; *b*, a style passed into the coronary vein, which, though it has no connexion with the left auricle, is, from its position, necessarily cut across in thus laying open the auricle *m.v.*

M.V. the two flaps of the mitral valve (drawn somewhat diagrammatically); *pp*, papillary muscles, belonging as before to the part of the ventricle cut away; *c*, a style passed from ventricle in *Ao.* aorta; *Ao*1. branch of aorta (see Fig. 12, *A'o'*); *P.A.* pulmonary artery; *S.V.C.* superior vena cava.

1, wall of ventricle cut across; 2, wall of auricle cut away around auriculo-ventricular orifice; 3, other portions of auricular wall cut across; 4, mass of fat around base of ventricle (see Fig. 12, 2).

poured into the upper ends of the vessel will cause its valves to close tightly, and allow nothing to flow out after the first moment.

Thus the arrangement of the auriculo-ventricular valves is such, that any fluid contained in the chambers of the heart can be made to pass through the auriculo-ventricular apertures in one direction only; that is to say, from the auricles to the ventricles. On the other hand, the arrangement of the semilunar valves is such that the fluid con-

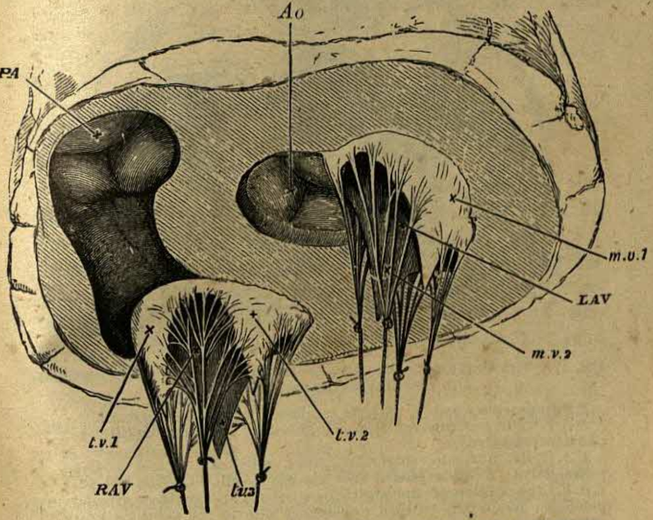

FIG. 18.—VIEW OF THE ORIFICES OF THE HEART FROM BELOW, THE WHOLE OF THE VENTRICLES HAVING BEEN CUT AWAY.

R.A.V. right auriculo-ventricular orifice surrounded by the three flaps, *t.v.* 1, *t.v.* 2, *t.v.* 3, of the tricuspid valve; these are stretched by weights attached to the *chordæ tendineæ*.

L.A.V. left auriculo-ventricular orifice surrounded in same way by the two flaps, *m.v.* 1, *m.v.* 2, of mitral valve; *P.A.* the orifice of pulmonary artery, the semilunar valves having met and closed together; *Ao.* the orifice of the aorta with its semilunar valves. The shaded portion, leading from *R.A.V.* to *P.A.*, represents the funnel seen in Fig. 16.

tents of the ventricles pass easily into the aorta and pulmonary artery, while none can be made to travel the other way from the arterial trunks to the ventricles.

6. The Beat of the Heart.—Like all other muscular tissues, the substance of the heart is contractile; but, unlike most muscles, the heart contains within itself a some-

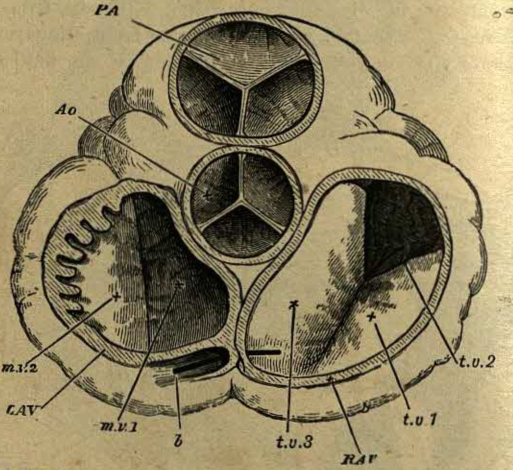

FIG. 19.—THE ORIFICES OF THE HEART SEEN FROM ABOVE THE AURICLES AND GREAT VESSELS BEING CUT AWAY

P.A. pulmonary artery, with its semilunar valves; *Ao.* aorta do.
R.A.V. right auriculo-ventricular orifice with the three flaps (*t.v.* 1, 2, 3) of tricuspid valve.
L.A.V. left auriculo-ventricular orifice, with *m.v.* 1 and 2, flaps of mitral valve; *b*, style passed into coronary vein. On the left part of *L.A.V.*, the section of the auricle is carried through the auricular appendage; hence the toothed appearance due to the portions in relief cut across.

thing which causes its different parts to contract in a definite succession and at regular intervals. The whole of the heart is not alike in its faculty for contracting spontaneously. Indeed this faculty of initiating the contraction is normally confined to a quite small portion. Starting here the contraction spreads over the auricle by a species of conduction, from the auricle it spreads on

over a delicate bridge of tissue, which is the functional connection between the auricle and the ventricle, and finally the whole ventricle becomes involved.

If the heart of a living animal be removed from the body, it will, if its substance is fed with a suitable nutrient fluid, go on beating much as it did while in the body. And careful attention to these beats will show that they consist of :—(1) A simultaneous contraction of the walls of both auricles. (2) Immediately following this, a simultaneous contraction of the walls of both ventricles. (3) Then comes a pause, or state of rest; after which the auricles and ventricles contract again in the same order as before, and their contractions are followed by the same pause as before.

The state of contraction of the ventricle or auricle is called its *systole*; the state of relaxation, during which it undergoes dilation, its *diastole*.

If the auricular contraction be represented by A˘, the ventricular by V˘, and the pauses by —, the series of actions will be as follows: A˘V˘ — A˘V˘ — A˘V˘ — &c. Thus the contraction of the heart is **rhythmical,** two short contractions of its upper and lower halves respectively being followed by a pause of the whole, which occupies nearly as much time as the two contractions.

The movements taking place in the heart during one complete beat and the pause are usually spoken of as a "cardiac cycle." This cycle is repeated, or as we more ordinarily say, "the heart beats" in an average healthy adult person about 72 times in a minute. From this it follows that the ordinary duration of each beat is $\frac{8}{10}$ of a second. Of this period the contraction of the auricles occupies $\frac{1}{10}$ and that of the ventricles $\frac{3}{10}$, the remaining $\frac{4}{10}$ being taken up by the pause of the heart as a whole. During each cycle or beat the heart undergoes certain changes of shape and position, as to the details of which there is some uncertainty, but which are, on the whole, as follows. During each systole

the width of the heart from side to side becomes less ; probably also the depth from back to front is at the same time slightly increased. The result of this is that whereas during diastole the shape of a section of the base of the ventricles is elliptical, during systole it becomes much more nearly circular.

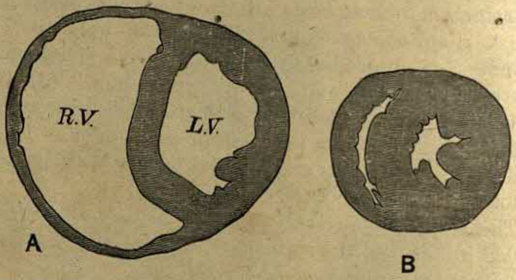

FIG. 20.—TRANSVERSE SECTION THROUGH THE MIDDLE OF THE VENTRICLES OF A DOG'S HEART IN DIASTOLE AND IN SYSTOLE. (AFTER HESSE.)

R.V. right ventricle; *L.V.* left ventricle.

The length of the heart is very slightly lessened, if at all, during systole, but the heart as a whole is twisted to a certain extent on its long axis, from the left and behind towards the front and right. The apex is at the same time tilted slightly forward and is hence pressed rather more firmly against the wall of the thorax, a fact of some importance in connection with what we shall describe presently as the "cardiac impulse" (see p. 57).

7. The Action of the Valves.—Having now acquired a notion of the arrangement of the different pipes and reservoirs of the circulatory system, of the position of the valves, and of the rhythmical contractions of the heart, it will be easy to comprehend what must happen if, when the whole apparatus is full of blood, the first step in the pulsation of the heart occurs and the auricles contract.

By this action each auricle tends to squeeze the fluid which it contains out of itself in two directions—the one towards the great veins, the other towards the ventricles ; and the direction which the blood, as a whole, will take,

will depend upon the relative resistance offered to it in these two directions. Towards the great veins it is resisted by the mass of the blood contained in the veins. Towards the ventricles, on the contrary, there is no resistance worth mentioning, inasmuch as the valves are open, the walls of the ventricles, in their uncontracted state, are flaccid and easily distended, and the entire pressure of the arterial blood is taken off by the semilunar valves, which are necessarily closed. The return of blood into the veins is further checked by a contraction of the great veins at their point of junction with the heart which immediately precedes the systole of the auricles, and is practically continuous with it.

Therefore, when the auricles contract, little or none of the fluid which they contain will flow back into the veins; all the contents or nearly so will pass into and distend the ventricles. As the ventricles fill and begin to resist further distension, the blood, getting behind the auriculo-ventricular valves, will push them towards one another, and indeed almost shut them. The auricles now cease to contract, and immediately that their walls relax, fresh blood flows from the great veins and slowly distends them again.

But the moment the auricular systole is over, the ventricular systole begins. The walls of each ventricle contract vigorously, and the first effect of that contraction is to complete the closure of the auriculo-ventricular valves and so to stop all egress towards the auricle. The pressure upon the valves becomes very considerable, and they might even be driven upwards, if it were not for the *chordæ tendineæ* which hold down their edges.

As the contraction continues and the capacities of the ventricles become diminished, the points of the wall of the heart to which the *chordæ tendineæ* are attached approach the edges of the valves; and thus there is a tendency to allow of a slackening of these cords, which, if it really took place, might permit the edges of the valves

to flap back and so destroy their utility. This tendency, however, is counteracted by the *chordæ tendineæ* being connected, not directly to the walls of the heart, but to those muscular pillars, the *papillary muscles*, which stand out from its substance. These muscular pillars shorten at the same time as the substance of the heart contracts; and thus, just so far as the contraction of the walls of the ventricles brings the *papillary muscles* nearer the valves, do they, by their own contraction, pull the *chordæ tendineæ* as tight as before.

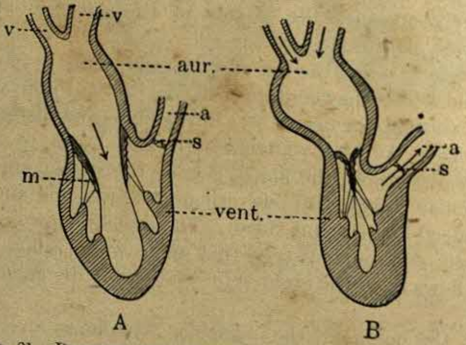

FIG. 21.—DIAGRAM TO ILLUSTRATE THE ACTION OF THE HEART.
aur. auricle; *vent.* ventricle; VV. veins; *a*, aorta; *m*, mitral valve; *s*, semilunar valve.
In A the auricle is contracting, ventricle dilated, mitral valve open, semilunar valves closed. In B the auricle is dilated, ventricle contracting, mitral valve closed, semilunar valves open.

By the means which have now been described, the fluid in the ventricle is debarred from passing back into the auricle; the whole force of the contraction of the ventricular walls therefore is expended in overcoming the resistance presented by the semilunar valves. This resistance is partly the result of the mere weight of the vertical column of blood which the valves support; but is chiefly due to the reaction of the distended elastic walls of the

great arteries, for as we shall see, these arteries are already so full that the blood within them is pressing on their walls with great force.

It now becomes obvious why the ventricles have so much more to do than the auricles, and why valves are needed between the auricles and ventricles, while none are wanted between the auricles and the veins.

All that the auricles have to do is to fill the ventricles, which offer no active resistance to that process. Hence the thinness of the walls of the auricles, and hence the needlessness of any auriculo-venous valve, the resistance on the side of the ventricle being so insignificant that it gives way, at once, before the pressure of the blood in the veins.

On the other hand, the ventricles have to overcome a great resistance in order to force fluid into elastic tubes which are already full; and if there were no auriculo-ventricular valves, the fluid in the ventricles would meet with less obstacle in pushing its way backward into the auricles and thence into the veins, than in separating the semilunar valves. Hence the necessity, firstly, of the auriculo-ventricular valves; and, secondly, of the thickness and strength of the walls of the ventricles. And since the aorta, systemic arteries, capillaries, and veins form a system of tubes, which, from a variety of causes, offer more resistance than do the pulmonary arteries, capillaries, and veins, it follows that the left ventricle needs a thicker muscular wall than the right.

Thus, at every systole of the auricles, the ventricles are filled and the auricles emptied, the latter being slowly refilled by the pressure of the fluid in the great veins, which is amply sufficient to overcome the passive resistance of the relaxed auricular walls. And, at every systole of the ventricles, the arterial systems of the body and lungs receive the contents of these ventricles, and the emptied ventricles remain ready to be filled by the auricles.

8. The Working of the Arteries.—We must now consider what happens in the arteries when the contents of the ventricles are suddenly forced into these tubes (which, it must be recollected, are already full).

If the vessels were tubes of a rigid material, like gas-pipes, the forcible discharge of the contents of the left ventricle into the beginning of the aorta would send a shock, travelling with great rapidity, right along the whole system of tubes, through the arteries into the capillaries, through the capillaries into the veins, and through these into the right auricle; and just as much blood would be driven from the end of the veins into the right auricle as had escaped from the left ventricle into the beginning of the aorta; and that, at almost the same instant of time. And the same would take place in the pulmonary vessels between the right ventricle and left auricle.

However, the vessels are not rigid, but, on the contrary, very yielding tubes; and the great arteries, as we have seen, have especially elastic walls. On the other hand, the *friction* in the small arteries and capillaries which opposes a resistance to the flow of blood, and is hence spoken of as the **peripheral resistance**, is so great that the blood cannot pass through them into the veins as quickly as it escapes from the ventricle into the aorta. Hence the contents of the ventricle, driven by the force of the systole past the semilunar valves, are at first lodged in the first part of the aorta, the walls of which are stretched and distended by the extra quantity of blood thus driven into it. But as soon as the ventricle has emptied itself and no more blood is driven out of it to stretch the aorta, the elastic walls of this vessel come into play; they strive to go back again and make the tube as narrow as it was before; thus they return back to the blood the pressure which they received from the ventricle. The effect of this elastic recoil of the arterial walls is on the one hand to

close the semilunar valves, and so prevent the return of blood to the heart, and, on the other hand, to distend the next portion of the aorta, driving an extra quantity of blood into it. And this second portion, in a similar way, distends the next, and this again the next, and so on, right through the whole arterial system. Thus the impulse given by the ventricle travels like a wave along the arteries distending them as it goes, and ultimately forcing the blood through the capillaries into the veins, and so on to the heart again.

Several of the practical results of the working of the heart and arteries just described now become intelligible.

9. **The Cardiac Impulse.**—If a finger be placed on the chest over the space between the fifth and sixth ribs on the left side, about one inch below the left nipple and slightly towards the sternum, a certain throbbing movement is perceptible, which is known as the "cardiac impulse." It is the result of the heart-beat making itself felt through the wall of the chest at this point, at the moment of the systole of the ventricles. Even when the heart is at rest the apex, in a standing position, lies close under and in contact with this part of the chest-wall. When the systole takes place the muscular substance of the ventricles becomes suddenly hard and tense, as do all muscles when they contract. At the same time the apex of the heart, as the result of the peculiar movements already described (p. 52), is brought into still firmer contact with the chest-wall. The cardiac impulse is the outcome of this sudden hardening of the ventricular walls, aided by their closer contact with the wall of the chest at the moment when the hardening takes place. It is *not* due, as is so frequently stated, to the heart "striking" or "tapping" against the chest-wall.

10. **The Sounds of the Heart.**—If the ear be applied over the heart, certain *sounds* are heard, which recur with great regularity, at intervals corresponding with those between every two beats. First comes a longish dull

booming sound; then a short sharp sound, then a pause, then the long, then the sharp sound, then another pause; and so on. These sounds are usually likened to the pronunciation of the syllables "lŭbb," "dŭp." There are many different opinions as to the cause of the first sound; some physiologists regard it as a muscular sound caused by the contraction of the muscular fibres of the ventricle, while others believe it to be due to the vibration of the auriculo-ventricular valves, when they become suddenly tense or stretched as the ventricles begin to contract. In reality the first sound has probably a double origin, being partly muscular and partly valvular, and this view is borne out by the following facts. The sound is given out during the ventricular systole and is most plainly heard at the spot where the cardiac impulse is most readily felt. It is greatly altered in character and obscured in cases of disease, or experimental injury of the auriculo-ventricular valves; but on the other hand it may be heard, although modified, in a beating heart through whose cavities the passage of blood is temporarily prevented.

The second sound is without doubt caused by the membranes of the semilunar valves becoming tense, and thus thrown into vibrations, on their sudden closure at the end of the ventricular systole. This is proved by the facts that the sound is loudest at that point on the chest-wall under which the semilunar valves lie; that it is modified and obscured by disease of these valves; and that it may be made to cease by experimentally hooking back the semilunar valves in a living animal.

11. Blood-pressure.—When an artery is cut, the outflow of blood is not uniform and smooth, but takes place in *jerks* which correspond to each beat of the heart. Moreover the blood *spurts out with considerable force*, which although it is greater at each jerk is still persistent and large between the jerks. The obvious conclusion to be drawn from the above observation is that the blood in

the artery is always under considerable, though variable, pressure. This pressure is called **blood-pressure.** We have already explained how this pressure comes to be established; but its importance is so great as a factor in the circulation that we may with advantage refer to this point once more.

The smallest arteries and capillaries offer a considerable frictional resistance to the flow of blood through them into the veins, called as we have already said, "peripheral resistance." Owing to this resistance, of the total amount of blood forced into the arteries at each beat of the heart, only a portion can during the actual beat, apart from the pause between it and the next beat, pass on into the veins. The remainder is lodged in the arteries whose walls, being distensible, are *put on the stretch by the pressure of the blood thrust into them at each stroke of the heart*, and this pressure of the blood on the arterial wall is what we mean by "blood-pressure." As soon as the arterial walls are stretched their *elastic* properties come into play; they *recoil* and press on the blood with a force equal to that which puts them on the stretch. This elastic recoil squeezes the blood on in the intervals between the successive beats of the heart, and thus renders the circulation continuous. In short the whole arterial system is always in a state of distension; the work of the heart consists in keeping up this distended condition by thrusting fresh blood into the arteries under pressure; and the pressure thus established forces the blood through the capillaries, on through the veins, and so back to the heart.

Blood-pressure is greatest in the large arteries near the heart and diminishes *gradually* along the arterial system until we come to the smallest arteries and capillaries; here the pressure falls *suddenly*. The sudden fall of pressure is due to the existence of what we have already referred to as "peripheral resistance." This resistance must be overcome in order to drive the blood on into the

veins; to overcome a resistance work must be done, and to do work, force must be employed and energy expended. Now blood-pressure is the force available for overcoming the resistance, and if it be thus used up there is less of it left, or in other words the pressure falls. In the veins the blood-pressure is still less than in the capillaries, and diminishes gradually along their course towards the heart.

These differences of pressure in the several parts of the vascular system determine the flow of blood along the vessels; the blood is always flowing from a higher to a lower pressure; the main work of the heart is to establish the large blood-pressure existing in the larger arteries.

When a vein is cut the blood does not spurt out as it does from a cut artery but oozes or trickles out gently, the reason being that the pressure in the veins is small. Further the flow is in this case continuous and not jerky as it is from a cut artery, in correspondence with the fact that there is no "pulse" in the veins as there is in the arteries. But this statement requires that we should next consider the nature and causes of the pulse.

12. **The Pulse.**—If the finger be placed on an artery which lies near the surface of the body, such as the *radial artery* at the wrist, what is known as the pulse will be felt as a slight throbbing pressure on the finger, coming and going at regular intervals which correspond to the successive beats of the heart. What is felt is in reality the intermittent rise and fall of that piece of the arterial wall which lies immediately under the finger. This fact may be easily proved by placing a light lever so as to rest over the artery, whereupon its end may be *seen* to rise and fall at the same regular intervals. This movement of the arterial wall is due to that distension of the arteries, of which we have already spoken, which is started at each beat of the heart by the extra quantity of blood driven into them by the ventricle, then travels in the form of a wave from the larger to the smaller arteries, and corre-

sponds to the jerky outflow of blood from a cut artery.

The pulse which is felt by the finger does not correspond in time precisely with the beat of the heart, but takes place a little after it, and the delay is longer, the greater the distance of the artery from the heart. For example, the pulse in the *tibial artery* on the inner side of the ankle is a little later than the pulse in the *temporal artery* in the temple. By suitable instruments the rate at which the pulse travels along the arteries may be readily determined and is found to be about 30 feet per second. This rate of progression of the pulse-wave must be carefully distinguished from the rate at which the blood is flowing along the artery. Even in the aorta, where the blood flows most rapidly (p. 64), the velocity is not more than about 15 inches per second. In fact "the pulse-wave travels over the moving blood somewhat as a rapidly moving natural wave travels along a sluggishly flowing river."

Under ordinary circumstances, the pulse is no longer to be detected in the capillaries, or in the veins. Sometimes a backward pulse from the heart along the great venous trunks may be observed; but this is quite another matter, and is the result of the movements of breathing. (See Lesson IV.) This actual loss, or rather transformation of the pulse is effected *by means of the elasticity of the arterial walls, called into play by the peripheral resistance*, in the following manner.

In the first place it must be borne in mind that, owing to the minute size of the small arteries and capillaries, the amount of friction taking place in their channels when the blood is passing through them is very great; in other words, they offer a very great resistance to the passage of the blood. The consequence of this is, that, in spite of the fact that the total area of the capillaries is so much greater than that of the aorta, the blood has a difficulty in getting through the capillaries into the veins as fast as it

is thrown into the arteries by the heart. The whole arterial system, therefore, becomes over-distended with blood.

Now we know by experiment that under such conditions as these, an elastic tube has the power, if long enough and elastic enough, to change a jerked impulse into a continuous flow.

If an ordinary syringe or other convenient form of pump be fastened to one end of a long glass tube, and water be forced through the tube, it will flow from the far end in jerks, corresponding to the jerks of the syringe. This will be the case whether the tube be quite open at the far end, or drawn out to a fine point so as to offer great resistance to the outflow of the water. The glass tube is a rigid tube, and there is no elasticity to be brought into play.

If now a long india-rubber tube be substituted for the glass tube, it will be found to act differently, according as the opening at the far end is wide or narrow. If it is wide, the water flows out in jerks, nearly as distinct as those from the glass tube. There is little resistance to the outflow, little distension of the india-rubber tube, little elasticity brought into play. If, however, the opening be narrowed, as by fastening to it a glass tube drawn out to a fine point, or if a piece of sponge be thrust into the end of the tube—if, in fact, in any way resistance be offered to the outflow of the water, the tube becomes distended, its elasticity is brought into play, and the water flows out from the end, not in jerks but in a stream, which is more and more completely continuous the longer and more elastic the tube, and the greater the resistance at its open end.

Substitute for the syringe the heart, for the finely drawn glass tube or sponge the small arteries and capillaries, for the india-rubber tube the whole arterial system, and you have exactly the same result in the living body. Through the action of the elastic arterial walls the separate

jets from the heart are blended into one continuous stream. The whole force of each blow of the heart is not at once spent in driving a quantity of blood through the capillaries; a part only is thus spent, the rest goes to distend the elastic arteries. But during the interval between that beat and the next the distended arteries are narrowing again, by virtue of their elasticity, and so are pressing the blood on into the capillaries with as much force as they were themselves distended by the heart. Then comes another beat, and the same process is repeated. At each stroke the elastic arteries shelter the capillaries from part of the sudden blow, and then quietly and steadily pass on that part of the blow to the capillaries during the interval between the strokes.

The larger the amount of elastic arterial wall thus brought into play, *i.e.* the greater the distance from the heart, the greater is the fraction of each heart's stroke which is thus converted into a steady elastic pressure between the beats. Thus the pulse becomes less and less marked the farther you go from the heart; any given length of the arterial system, so to speak, being sheltered by the lengths between it and the heart.

Every inch of the arterial system may, in fact, be considered as converting a small fraction of the heart's jerk into a steady pressure, and when all these fractions are summed up together in the total length of the arterial system no trace of the jerk is left.

As the immediate, sudden effect of each systole becomes diminished in the smaller vessels by the causes above mentioned, the influence of this constant pressure becomes more obvious, and gives rise to a steady passage of the fluid from the arteries towards the veins. In this way, in fact, the arteries perform the same functions as the air-reservoir of a fire-engine, which converts the jerking impulse given by the pumps into the steady flow from the nozzle of the delivery hose.

The phenomena so far described are the direct outcome

of the mechanical conditions of the organs of the circulation combined with the rhythmical activity of the heart. This activity drives the fluid contained in these organs out of the heart into the arteries, thence to the capillaries, and from them through the veins back to the heart. And in the course of these operations it gives rise, incidentally, to the cardiac impulse, the sounds of the heart, blood-pressure, and the pulse.

13. The Rate of Blood Flow.—It has been found, by experiment, that in the horse it takes about half a minute for any substance, as for instance a chemical body, whose presence in the blood can easily be recognized, to complete the circuit, *ex. gr.* to pass from the jugular vein down through the right side of the heart, the lungs, the left side of the heart, up through the arteries of the head and neck, and so back to the jugular vein.

By far the greater portion of this half minute is taken up by the passage through the small vessels, where the blood moves, it is estimated, at the rate only of about one and a half inches in a *minute*, whereas through the carotid artery of a dog it flies along at the rate of about ten inches in a *second*. Of course to complete the circuit of the circulation, a blood-corpuscle need not have to go through so much as half of an inch of capillaries in either the lungs or any of the tissues of the body.

Inasmuch as the force which drives the blood on is (putting the other comparatively slight helps on one side) the beat of the heart and that alone, however much it may be modified, as we have seen, in character, it is obvious that the velocity with which the blood moves must be greatest in the aorta and diminish towards the capillaries.

For with each branching of the arteries the total area of the arterial system is increased, the total width of the capillary tubes if they were all put together side by side being very much greater than that of the aorta. Hence the blood, or a corpuscle, for instance, of the blood being

driven by the same force, viz. the heart's beat, over the whole body, must pass much more rapidly through the aorta than through the capillary system or any part of that system.

It is not that the greater friction in any capillary causes the blood to flow more slowly there and there only. The resistance caused by the friction in the capillaries is thrown back upon the aorta, which indeed feels the resistance of the whole vascular system; and it is this total resistance which has to be overcome by the heart before the blood can move on at all.

The blood driven everywhere by the same force simply moves more and more slowly as it passes into wider and wider channels. When it is in the capillaries it is slowest; after escaping from the capillaries, as the veins unite into larger and larger trunks, and hence as the total venous area is getting less and less, the blood moves again faster and faster for just the same reason that in the arteries it moved slower and slower. It is, in fact, *the differences in the width of the "bed,"* and this alone, which determines the differences in the rate of flow at the various points of the vascular system.

A very similar case is that of a river widening out in a plain into a lake and then contracting into a narrow stream again. The water is driven by one force throughout (that of gravity). The current is much slower in the lake than in the narrower river either before or behind.

14. The Nervous Control of the Arteries. Vaso-motor Nerves.—The arteries, as we have seen, are characterised structurally by being elastic and muscular. In the large arteries the elastic properties are more marked than the muscular, whereas in the smaller arteries the muscular tissue is present in large amount relatively to the elastic elements; and we have dealt in detail with the significance of arterial elasticity and its use in connection with the establishment of blood pressure and the disappearance of the pulse. It has also been pointed out

(p. 34) that the small arteries may be directly affected by the nervous system, which controls the state of contraction of their walls, and regulates their calibre, and thus governs the supply of blood to each part of the body according to its varying needs. The control of the nervous system over the circulation in particular spots is of such paramount importance that we must now deal with this also in some detail.

A phenomenon with which every one is more or less familiar, either as experienced on themselves or observed on other persons, is that known as **blushing**. Now blushing is a purely *local* modification of the circulation, and it will be instructive to consider how a blush is brought about. An emotion, sometimes pleasurable, sometimes painful, takes possession of the mind; thereupon a hot flush is felt, the skin grows red, and according to the intensity of the emotion these changes are confined to the cheeks only, or extend to the "roots of the hair," or "all over."

What is the cause of these changes? The blood is a red and a hot fluid; the skin reddens and grows hot, because its vessels contain an increased quantity of this red and hot fluid; and its vessels contain more, because the small arteries suddenly dilate, the natural moderate contraction of their muscles being superseded by a state of relaxation; and this relaxation comes on because the action of the nervous system which previously kept the muscles in a state of moderate contraction is, for the time, suspended.

On the other hand, in many people, extreme terror or rage causes the skin to grow cold, and the face to appear pale and pinched. Under these circumstances, in fact, the supply of blood to the skin is greatly diminished, in consequence of an increased contraction of the muscles of the small arteries whereby these become unduly narrowed or constricted, and thus allow only a small quantity of blood to pass through them; and this increased con-

traction of the muscular coats of the arteries is brought about by the increased action of the nervous system.[1]

That this is the real state of the case may be proved experimentally upon rabbits. These animals may be made to blush artificially. If, in a rabbit, the **sympathetic nerve** (Fig. 22, *C. Sy.*), which sends branches to the vessels of the head is cut, the ear of the rabbit, which is covered by so delicate an integument that the changes in its vessels can be readily perceived, at once blushes. That is to say, the vessels dilate, fill with blood, and the ear becomes red and hot. The reason of this is, that when the sympathetic is cut, the nervous impulse which is ordinarily sent along its branches is interrupted, and the muscles of the small vessels, which were previously slightly contracted, become altogether relaxed.

And now it is quite possible to produce pallor and cold in the rabbit's ear. To do this it is only necessary to irritate the cut end of the sympathetic which remains connected with the vessels. The nerve then becomes excited, so that the muscular fibres of the vessels are thrown into a violent state of contraction, which diminishes their calibre so much that the blood can hardly make its way through them. Consequently, the ear becomes pale and cold.

This experiment on the blood-vessels of the rabbit's ear is of fundamental importance as proof of the existence of nerves which control locally the muscular elements of the walls of the smaller arteries; and inasmuch as this control consists in causing *movements* of the walls of the *vessels*, by means of which their calibre is regulated, the nerves which exert the control receive the general name of **vaso-motor** nerves. But from the fact that when the cut end of the sympathetic nerve is irritated, or, as the physiologist says, is "stimulated," the muscular walls

[1] Sudden paleness is perhaps most frequently due to a failure or stoppage of the heart's beat, as in fainting. But it may also be observed when there is no change in the beat of the heart

of the arteries with which it is connected are always contracted and the vessels themselves constricted, the sympathetic is more precisely characterised as a **vaso-constrictor nerve.** Further, since merely cutting the sympathetic leads to a dilation of the blood-vessels of the ear, we are justified in assuming that vaso-constrictor impulses are *continually being sent out* along this nerve, whereby the arteries are kept continually in a condition of slight or medium constriction. To this condition the name is given of **arterial "tone."** Now this "tone" is of great importance, for by its existence it at once becomes possible to increase the blood-supply to any part of the body as well as to diminish it. Did the arteries possess no "tone" they would, under ordinary resting conditions, be dilated to their full extent, and the part or organ they supply with blood would be receiving a maximum supply when at rest. But the organs of the body are never at rest for long, and when they become active they require an increased amount of blood which could not be supplied, at least by a vaso-constrictor mechanism, but for the existence of this arterial tone. It would of course be possible to increase the blood-supply by means of an increased activity of the heart; but this would affect the supply to every part of the body at the same time, and what is really wanted is a localised variation in supply to meet the varying needs of each part or organ. Thus the vaso-constrictor nerves act by carrying *more* or *less* of the *same kind of impulse*, leading to increase or loss of tone and hence lessened or increased blood-supply; they do not act, as is so frequently and erroneously imagined, by carrying one set or kind of impulses to produce constriction, and another set or kind to produce dilation.

We have quoted blushing as being a characteristic and familiar instance of the action of vaso-motor (vaso-constrictor) nerves. But other examples of exactly similar action are met with throughout the whole body. Thus when a muscle contracts, or when a salivary gland secretes

saliva, or when the stomach is preparing to digest food, in each case the small arteries of the muscle, salivary gland or stomach, dilate and so flush the part with blood. The organ in fact blushes; and this inner unseen blushing may, like the ordinary blushing described above, be brought about by vaso-motor nerves. It may also be brought about by chemical bodies produced in the organs, which, acting on the muscular walls of their arteries, cause them to relax. We shall see later on that the temperature of the body is largely regulated by the supply of blood sent to the skin to be cooled, and this supply is in turn regulated by the vaso-motor nervous system. Indeed everywhere all over the body, the nervous system by its vaso-motor nerves is continually supervising and regulating the supply of blood, sending now more now less blood, to this or that part; and many diseases, such as those when exposure to cold causes congestion or inflammation, are due to, or at least associated with, a disorder or failure of this vaso-motor activity.

15. **The Vaso-motor Centre.**—The vaso-constrictor nerves, which, by causing the varying contraction in the muscular walls of the arteries, thus control the supply of blood to each region of the body, can all be traced back to the spinal cord. They make their exit from this part of the central nervous system by the anterior roots of the spinal nerves of the middle part of the cord, and after passing through the ganglia of the sympathetic system (see Lesson XI.) are distributed to their various destinations. The impulses which these nerves convey to the blood-vessels are of course received by them from the spinal cord. This being the case the interesting question arises as to where these impulses are generated before their exit from the cord. Experiment shows that under ordinary circumstances they come down the cord from a point higher up, *i.e.* nearer the brain, than that at which the nerves themselves pass off from the cord. In fact it has been shown that they originate in a very limited portion of the central nervous system, located in that part

of it which we shall describe in a later Lesson (XI.) as the **spinal bulb** or **medulla oblongata.** Here then the vaso-constrictor impulses are generated, and since they are the chief agents in determining the state of contraction or relaxation of the arteries of the body as a whole, this definitely localised part of the bulb has received the name of the **vaso-motor centre.** (Fig. 22, *V.M.C.*).

The cause of the phenomenon of arterial "tone" now becomes quite clear. The vaso-motor centre continually generates and sends out impulses to every part, or rather to very many parts, of the body, which suffice to keep the muscle fibres of the arteries supplying those parts in a condition of slight contraction. When the impulses are increased to any part, the supply of blood to that part is lessened; when the impulses are lessened the supply is increased.

But if the vaso-motor centre is to be of use it must itself be under the influence of impulses which can be made to play upon it in such a way as to determine those variations in its activity which are essential to its adapting itself to the varying needs of either the body as a whole or any small part of the body. These impulses which govern the vaso-motor centre pass into it either down from the brain above, or up from the spinal cord below. As an instance of the former case we may refer once again to "blushing." Here the emotion which leads to the blush, starts impulses in the brain which then pass down to the vaso-motor centre and modify its activity so as to lessen the intensity of the impulses it sends to the blood-vessels of the cheeks. As an instance of the second case we may refer to the effects of heat and cold applied to the body, as determining those variations of blood-supply to the skin by which the temperature of the body is so largely regulated (see Lesson V.). Here the impulses are started in the skin and, travelling along certain sensory nerves, enter the spinal cord, pass up to the vaso-motor centre, and as before lead to the necessary changes in its activity.

16. Vaso-dilator Nerves.—Our consideration of vaso-motor nerves has so far led us to the view that the dilation or widening of an artery which leads to increase blood-

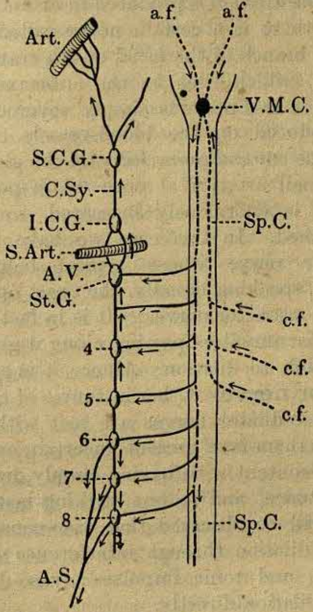

FIG. 22.—DIAGRAM TO ILLUSTRATE THE POSITION OF THE VASO-MOTOR CENTRE, THE PATHS OF VASO-CONSTRICTOR IMPULSES FROM THE CENTRE ALONG THE CERVICAL SYMPATHETIC NERVE AND (PART OF) THE ABDOMINAL SPLANCHNIC, AND THE COURSE OF IMPULSES TO THE CENTRE FROM THE BRAIN AND FROM AN OUTLYING PART OF THE BODY.

Sp.C., *Sp.C.* spinal cord; *V.M.C.* vaso-motor centre; *Art.* artery of ear; *C.Sy.* cervical sympathetic; *S.C.G.* superior cervical ganglion; *I.C.G* inferior cervical ganglion; *S.Art.* subclavian artery; *A.V.* annulus of Vieussens; *St.G.* stellate ganglion; 4, 5, 6, 7, 8, fourth, fifth, sixth, seventh and eighth thoracic ganglia; *A.S.* upper roots and part of abdominal splanchnic nerve. The dotted lines *a.f.*, *a.f.* indicate paths of conduction for impulses to the vaso-motor centre from the brain. The dotted lines *c.f.*, *c.f.*, *c.f.* indicate paths for the passage of impulses to the vaso-motor centre from some outlying part of the body such as the skin. The arrows show the directions in which the impulses travel along each path.

supply is usually the result of cutting off or lessening constrictor impulses which were previously passing along the nerves to the arteries. But instances are met with in the body where the dilation is produced in an entirely different way. Thus there is a certain nerve called the **chorda tympani**, a branch of the facial or 7th cranial nerve (see Lesson XI.), which runs to the submaxillary salivary glands. When this nerve is simply severed, no obvious effect is produced on the blood-vessels of the gland. But if now the cut *end connected with the gland be stimulated*, the small arteries at once dilate powerfully, the blood-supply is enormously increased, and the gland becomes flushed. In this case we have to deal with a vaso-motor nerve whose typical behaviour when stimulated is, speaking broadly, the exact opposite to that of the vaso-constrictor nerves. It is in fact a vaso-motor nerve such that impulses passing along it give rise not to constriction but to dilation. Hence it is spoken of as a **vaso-dilator nerve.** Other instances of the occurrence of similar vaso-dilator nerves are met with, but as our knowledge of them is at present uncertain and incomplete we must be content with having simply drawn attention to their existence, and to one striking instance of their action. It will be observed that vaso-constrictor nerves only lead to dilation through interference with the vaso-motor centre and tonic impulses; vaso-dilator nerves bring about dilation directly.

17. Nervous Control of the Heart. Cardiac Nerves. —The heart, as we all know, is not under the direct influence of the will, but every one is no less familiar with the fact that the actions of the heart are wonderfully affected by all forms of emotion. Men and women often faint, and have sometimes been killed by sudden and violent joy or sorrow; and when they faint or die in this way, they do so because the perturbation of the brain gives rise to a something which arrests the heart as dead as you stop a stop-watch with a

spring. On the other hand, other emotions cause that extreme rapidity and violence of action which we call palpitation. These facts suggest at once that the heart, like the arteries, is subject to control by the central nervous system, and we must now consider the more important details of this control.

The heart is well supplied with nerves. There are many small *ganglia*, or masses of nerve cells, lodged in the substance of the heart, more especially in the auricles, and nerves spread from these ganglia over the walls, both of the auricles and ventricles. Moreover, several nerves reach the heart from the outside (Fig. 23). Of these the most important are branches of a remarkable nerve which starts from the spinal bulb, and supplies not only the heart, but the lungs, alimentary canal, and other parts, and which is called the **pneumogastric**, or from its wandering course, the **vagus** (see Lesson XI.). Other nerves reaching the heart seem to come from the sympathetic, but may be traced back through the sympathetic to the spinal cord, and, for reasons which will presently become apparent, are called **accelerator nerves.**

The heart, as already explained (p. 51), contracts rhythmically, but the regular rhythmical succession of the ordinary contractions is not primarily dependent upon the ganglia lodged in its substance, as was at one time supposed to be the case. Neither does it depend on the action of the nerves connected with the heart, since the movements continue even after the heart is removed from the body. Hence we must conclude, and experiment bears out the conclusion, that *the muscle substance of which the heart is made is itself endowed with the power of contracting and relaxing at regular intervals.* On the other hand the influences which alter the heart's action, as in fainting or palpitation, do as a rule come to the heart from without, and are carried to the heart along the vagus and accelerator nerves. This may be demonstrated on animals, such as frogs, with great ease.

If a frog be pithed, or its brain be otherwise destroyed, so as to obliterate all sensibility, the animal will continue to live, and its circulation will go on perfectly well for a prolonged period. The body may be laid open without causing pain or other disturbance, and then the heart will be observed beating with great regularity. It is possible to make the heart move a long lever backwards and forwards; and if frog and lever are covered with a glass shade, the air under which is kept moist, the lever may vibrate with great steadiness for a couple of days.

It is easy to adjust to the frog thus prepared a contrivance by which electrical shocks may be sent through the vagus nerves, so as to stimulate them. If the stimulation is only gentle or weak, the heart will be seen to beat more slowly, and at the same time each beat is rather more feeble, as shown by the diminished distance over which the end of the lever moves. But if the stimulation is strong, the lever almost immediately stops dead, and the heart will be found quiescent, with relaxed and distended walls. After a little time the influence of the vagus passes off, the heart recommences its work as vigorously as before, and the lever vibrates through the same arc as formerly. With careful management, this experiment may be repeated very many times ; and after every arrest by the stimulation of the vagus, the heart resumes its work.

If on the other hand the stimulation be applied to the sympathetic nerves, then an effect is produced which is exactly the opposite to that which results from stimulating the vagus. The lever moves more rapidly and over a greater distance, showing quite clearly that the heart is now beating faster and that each beat is stronger.

No clearer proof could be desired than is afforded by the above experiments, that the heart of the frog is controlled by two antagonistic nerves of which one, the vagus, carries impulses which slow and finally stop its

beat, while the other, the accelerator, conveys impulses which make it beat faster. Since experiments have shown that the mechanism just described exists equally in the mammalian heart, we may at once apply these striking results to the human heart. It is, in fact, recorded of a certain well-known physiologist, that having a small hard tumour in his neck, in close proximity to the vagus nerve, he could press the vagus against this tumour and by thus stimulating it mechanically cause a stoppage of his own heart-beat.

The heart, then, is controlled by two kinds of antagonistic influences, analogous to those previously described as controlling the muscular walls of the arteries. Moreover both the cardiac nerves are connected with the central nervous system, the one coming from the spinal bulb, the other from the spinal cord, so that the influences they convey to the heart must, as in the case of the vaso-motor nerves, originate in the central nervous system. We saw, however (p. 69), that the impulses carried by the vaso-motor nerves are generated in a very specially localised part of the spinal bulb, and the interesting question at once arises: Is there a similarly localised centre in which the impulses which modify the beat of the heart take their origin? The answer to this question is in the affirmative, for experiment shows that the impulses which, travelling along the vagus, can stop or, as the physiologist says "inhibit," the heart's beat, are generated in a limited part of the spinal bulb, in close proximity to the vaso-motor centre. This part is therefore known as the **cardio-inhibitory centre.** There are reasons for supposing that this centre, like the vaso-motor centre, is continually at work sending out impulses to the heart along the vagus, which check its activity, so that in many animals the heart beats more quickly after the vagus nerves are cut.

The cardio-inhibitory centre may, like the vaso-motor

centre, be itself influenced by impulses which reach it either from the brain above or the spinal cord below. In

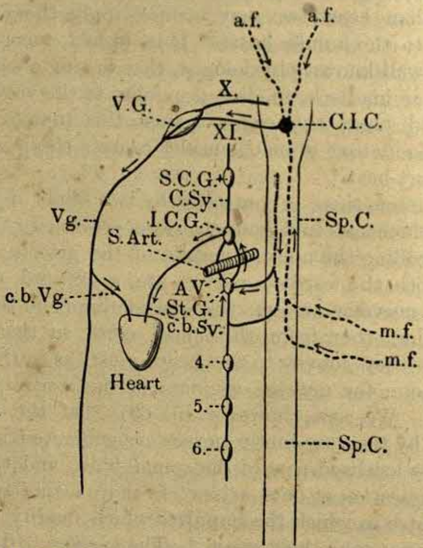

FIG. 23.—DIAGRAM TO ILLUSTRATE THE POSITION OF THE CARDIO-INHIBITORY CENTRE, THE PATHS OF INHIBITORY AND ACCELERATOR IMPULSES FROM THE CENTRAL NERVOUS SYSTEM TO THE HEART, AND THE COURSE OF IMPULSES TO THE CENTRE FROM THE BRAIN AND FROM AN OUTLYING PART OF THE BODY.

Sp.C., *Sp.C.* spinal cord; *C.I.C.* cardio-inhibitory centre; *X.* vagus nerve at its origin; *V.G.* ganglion of the vagus, through which run the fibres coming from the centre along *XI*, the spinal accessory nerve (see Lesson XI.). *Vg.* main trunk of the vagus; *c.b.Vg.* cardiac branches of vagus, supplying the heart; *C.Sy.* sympathetic nerve in the neck; *S.C.G.* superior cervical ganglion; *I.C.G.* inferior cervical ganglion; *S.Art.* subclavian artery; *A.V.* annulus of Vieussens; *St.G.* stellate ganglion; 4, 5, 6, fourth, fifth and sixth thoracic ganglia; *c.b.Sy.* cardiac branches of the sympathetic supplying the heart. The dotted lines *a.f.*, *a.f.* indicate paths of conduction for impulses to the cardio-inhibitory centre from the brain. The dotted lines *m.f.*, *m.f.* indicate paths for the passage of impulses to the cardio-inhibitory centre from some outlying part of the body such as the stomach or intestines. The arrows show the directions in which the impulses travel along each path.

this way the heart is indirectly connected with all parts of the body, so that by nervous agencies its beat may be made to vary. For instance when a person faints from a sudden emotion, an influence is started in the brain, passes down to the centre in the spinal bulb, *increases* its action and stops for a time the beating of the heart. Or again, fainting may result from a blow on the stomach; in this case the influence starts at the part struck, and passing up the spinal cord to the cardio-inhibitory centre, increases its activity and leads as before to stoppage of the heart. The rapid and violent beating of the heart which we speak of as "palpitation" may on the other hand be often due to some emotion which in this case *lessens* the activity of the centre and hence diminishes the restraint which it ordinarily exerts over the heart. But of course palpitation may also at times be due to impulses reaching the heart along those nerves which we have described above as the accelerators.

Our knowledge of the existence and position of the cardio-inhibitory centre is quite clear and definite. It is possible that a cardio-augmentor (-accelerator) centre may also exist, but at present we have no exact knowledge of its existence; hence in the accompanying figure (Fig. 23) the accelerator nerves are shown as originating in the central nervous system, but not arising from any definitely localised centre.

18. The Proofs of the Circulation.—The evidence that the blood circulates in man, although perfectly conclusive, is almost all indirect. The most important points in the evidence are as follows:—

In the first place, the disposition and structure of the organs of circulation, and more especially the arrangement of the various valves, will not, as was shown by Harvey, permit the blood to flow in any other direction

than in the one described above. Moreover, with a syringe, we can easily inject a fluid from the vena cava,

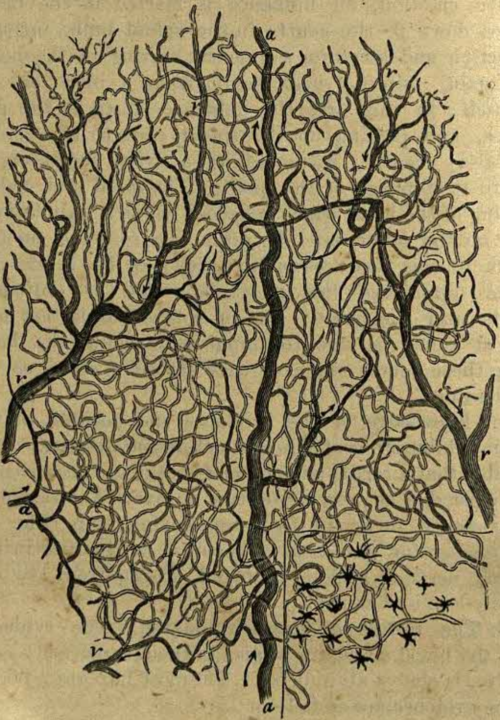

FIG. 24.—PORTION OF THE WEB OF A FROG'S FOOT SEEN UNDER A LOW MAGNIFYING POWER, THE BLOOD-VESSELS ONLY BEING REPRESENTED, EXCEPT IN THE CORNER OF THE FIELD, WHERE IN THE PORTION MARKED OFF THE PIGMENT SPOTS ARE ALSO DRAWN.

a, small arteries; *v*, small veins; the minute tubes joining the arteries of the veins are the capillaries. The arrows denote the direction of the circulation. The larger artery running straight up in the middle line breaks up into capillaries at points higher up than can be shown in the drawing.

through the right side of the heart, the lungs, the left side of the heart, the arteries, and capillaries, back to the vena cava ; but not the other way. In the second place, we know that in the living body the blood is continually flowing in the arteries towards the capillaries, because when an artery is tied, in a living body, it swells up and pulsates on the side of the ligature nearest the heart, whereas on the other side it becomes empty, and the tissues supplied by the artery become pale from the want of a supply of blood to their capillaries. And when we cut an artery the blood is pumped out in jerks from the cut end nearest the heart, whereas little or no blood comes from the other end. When, however, we tie a vein the state of things is reversed, the swelling taking place on the side farthest from the heart, &c., &c., showing that in the veins the blood flows from the capillaries to the heart.

But certain of the lower animals, the whole, or parts, of the body of which are transparent, readily afford direct proof of the circulation ; in these the blood may be seen rushing from the arteries into the capillaries, and from the capillaries into the veins, so long as the animal is alive and its heart is at work. The animal in which the circulation can be most conveniently observed is the frog. The web between its toes is very transparent, and the corpuscles suspended in its blood are so large that they can be readily seen as they slip swiftly along with the stream of blood, when the toes are fastened out, and the intervening web is examined under a microscope (Fig. 24).

19. **The Capillary Circulation.**—The essential characteristics of blood-flow through the capillaries may be easily studied by observation under the microscope of the web of a frog's foot. In the smallest capillaries the corpuscles pass along singly, sometimes following each other in close file, at other times leaving quite considerable

gaps in their succession. Frequently one or more corpuscles may remain stationary for a moment and then pass on again. The red corpuscles, which in the frog are oval and comparatively large, glide along with their long axis parallel to the direction of the stream, and may often be observed to be squeezed out of shape by pressure against the wall of the capillary (Fig. 25, *G* and *H*). In the larger capillaries, more especially in mammals whose corpuscles are smaller than in the frog, the corpuscles often pass along two or three abreast. Further, in these larger capillaries it may be seen that the red corpuscles tend to keep to the centre of the stream, leaving a clear layer of fluid along the sides of the blood-vessels. This is due to the fact that the fluid friction (already referred to on p. 56) is greater close to the walls of the capillaries than in the middle of the stream, and the corpuscles pass along where the resisting friction is least. The colourless or "white" corpuscles usually move more slowly and irregularly than the red, and may, as a rule, be seen to lie in the clearer layer of fluid at the side of the current. Moreover, they frequently stop for an appreciable time, as if sticking to the wall of the capillary, and then roll on again; probably because they are more adhesive than the red corpuscles as a result of their power of executing amœboid movements (see p. 100).

20. Inflammation.—Everybody is more or less familiar with a peculiar and unusual condition which may arise in almost any part of the body, and which they describe by speaking of the part as "inflamed." To ordinary observation the characteristics of the condition are that the inflamed region becomes flushed and red, that it feels warmer than usual, that it becomes swelled and painful, and finally, if the inflammation is severe, that a thick yellowish fluid is formed which is commonly known as "matter," or more correctly as **pus**. Such a series of changes may be observed during the formation and breaking of a boil. But the several stages just named are

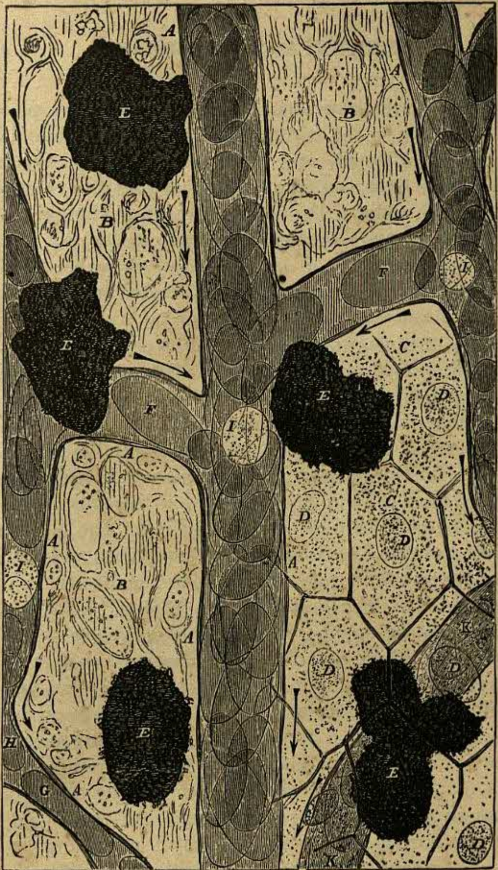

FIG. 25.—VERY SMALL PORTION OF FIG. 24 VERY HIGHLY MAGNIFIED.

A, walls of capillaries; *B*, tissue of web lying between the capillaries; *C*, cells of epidermis covering web (these are only shown in the right-hand and lower part of the field; in the other parts of the field the focus of the microscope lies below the epidermis); *D*, nuclei of these epidermic cells; *E*, pigment cells contracted, not partially expanded as in Fig. 24; *F*, red blood-corpuscle (oval in the frog) passing along capillary—nucleus not visible; *G*, another corpuscle squeezing its way through a capillary, the canal of which is smaller than its own transverse diameter; *H*, another bending as it slides round a corner; *K*, corpuscle in capillary seen through the epidermis; *I*, white blood-corpuscle.

merely the external evidences of changes taking place at the same time in the minute blood-vessels and circulation of the part affected, and since these changes throw an interesting light on the relations ordinarily existing between the walls of the blood-vessels and the neighbouring blood, they are worthy of a short consideration.

If when the web of a frog's foot, or other suitably transparent part of an animal, is adjusted for observation under the microscope, some irritant be applied to it such as a trace of mustard,[1] the following events may be readily observed. The minute arteries dilate, the blood flows faster, and the increased quantity of blood forced through the capillaries distends them so that they, as well as the smallest veins, appear to be similarly dilated. This accounts for the initial greater redness and warmth of an inflamed part. Very soon the colourless corpuscles are seen to be collecting in large numbers in the clear layer of fluid next to the walls of the capillaries and veinlets, and seem to adhere more firmly than usual to the walls of these vessels. Further, blood "platelets" (see p. 103), not previously visible, begin to collect also with and among the white corpuscles. Following upon this the stream of blood begins to flow more slowly although the blood-vessels are still widely dilated. And now a very striking phenomenon takes place. The white corpuscles make their way by amœboid movements through the thin walls of the capillaries and collect outside them in the spaces in the neighbouring tissue. At the same time that the corpuscles are in this way "migrating," a considerable quantity of the fluid part of the blood also passes out through the walls of the blood-vessels into the adjacent tissue. This accounts for the characteristic swelling of an inflamed part. If the action of the irritant is continued, more and more white corpuscles collect in the vessels, the blood-flow becomes slower and slower,

[1] Used similarly as an irritant in the form of the ordinary domestic mustard poultice.

red corpuscles are arrested in large numbers among the white, and finally the circulation stops altogether. At this stage red corpuscles pass through the walls of the vessels as well as the white, and the latter multiplying rapidly in the spaces of the tissue outside the blood-vessels, and undergoing certain other slight changes, are converted into pus corpuscles.

The appearances just described seem to indicate that *the condition of the walls of the capillaries* (and of the smallest veins and arteries) plays a very important part in determining the characteristics of the normal circulation through these passages. And since in an inflamed area the flow of blood becomes slower and slower, and ultimately ceases, even while the blood-vessels are more widely dilated than usual, the condition of the walls of these vessels may evidently play a very important part in determining variations in that "peripheral resistance" which, as we have previously explained, is of paramount importance to the working of the circulation throughout every part of the whole body. Moreover it is evident that the condition of the walls of the capillaries may also at any moment modify the amount of the fluid part of the blood which is continually passing out through those walls as lymph (p. 84) for the nutrition of the neighbouring tissues.

PART II.—THE LYMPHATIC SYSTEM AND THE CIRCULATION OF LYMPH

1. The General Arrangement of the Lymphatics.—Food, as we have already pointed out (p. 23), after digestion in the alimentary canal, is absorbed into the blood-vessels and lacteals of that canal and whirled away in the current of the circulation for distribution as nutritive material to all parts of the body. But we have also drawn attention to the fact (p. 31) that the ultimate

anatomical components, the cells and tissues, of every part of the body lie *outside* the blood-vessels. It is therefore clear that the tissues are everywhere separated from the blood by at least the thickness of the walls of the vessels, and in any case cannot draw the nutriment they require directly from the blood, since they are nowhere in direct contact with it. Neither can they, for the same reason, discharge the waste they are always producing directly into the blood for its removal as a preliminary to its excretion. Both these difficulties are however got over by the fact that *a portion of the fluid part of the blood is continually exuding through the walls of the capillaries* into the neighbouring tissues, taking with it the nutriment necessary for each tissue and providing a fluid connection between the tissue and the blood across which the waste from the tissues can be returned into the blood. The fluid which thus exudes is called **lymph**,[1] and may be regarded as a sort of "middleman" between the blood on the one hand and the tissue on the other. But if now this lymph is to be thoroughly efficient as a nutriment for the tissues it should presumably contain more food material than the tissues actually require as an average, and it must therefore be an economy to the body if the lymph, after having served the needs of the tissues, is gathered up again and returned to the blood for further use. Now this is exactly what does take place, and the means for ensuring the return of the lymph to the blood-vessels are as follows.

Besides the capillary network and the trunks connected with it which constitute the blood-vascular system, all parts of the body which possess blood capillaries also contain another set of what are termed **lymph-capillaries**, mixed up with those of the blood-vascular system, but not directly communicating with them, and, in addition differing from the blood-capillaries in being

[1] The mode of formation, composition and properties of lymph are dealt with in Lesson III.

connected with larger vessels of only one kind. That is to say they open only into trunks which carry fluid away from them, and thus bear the same relationship to the lymph-capillaries that the veins do to blood-capillaries. These trunks are known as the **lymphatic vessels,** and further resemble the small veins in the general structure of their walls and in being abundantly provided with valves, similar to those in the veins, which freely allow of the passage of lymph from the lymph-capillaries, but obstruct the flow of any liquid in the opposite direction. But the lymphatic vessels differ from the veins in that they do not rapidly unite into larger and larger trunks which present a continually increasing calibre and allow a flow without interruption to the heart. On the contrary, remaining nearly of the same size, they at intervals become connected with small rounded or often bean-shaped bodies called **lymphatic glands,** entering the glands at one side and emerging at the opposite side as new lymphatic vessels (Fig. 26, *g.*).

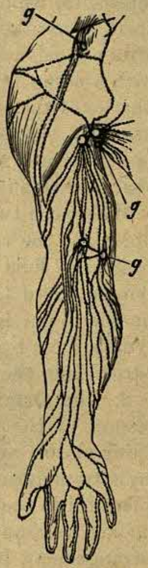

FIG. 26.—THE LYMPHATICS OF THE FRONT OF THE RIGHT ARM.
g, lymphatic glands, on the course of the lymphatics.

Sooner or later the great majority of the smaller lymphatic vessels pour their contents into a tube which is about as large as a goose-quill, lies in front of the backbone, and is called the **thoracic duct.** This opens at the root of the neck into the conjoined trunks of the great veins (jugular and subclavian) which bring back the blood from the *left* side of the head and the *left* arm. (Fig. 27, *f.g.*)

The remaining lymphatics, chiefly those of the right

side of the head and neck, the right arm and right lung, are connected by a common canal with the corresponding vein of the right side.

The lower part of the thoracic duct is dilated, and is called the **receptacle of the chyle** (Fig. 27, *a*.). This part receives more particularly the lymphatics from the intestines, which, though they differ in no essential respect from other lymphatics, are called **lacteals**, because, after a meal containing much fatty matter, they are filled with a *milky* fluid termed **chyle**. The lacteals, or lymphatics of the small intestine, not only form networks in its walls, but send blind prolongations into the little processes termed **villi**, with which the mucous membrane of that intestine is beset. (See Lesson VI.)

Where the two principal trunks of the lymphatic system open into the veins, valves are placed which allow of the passage of fluid in one direction only, namely from the lymphatic to the veins, the blood in the veins being unable to get into the lymphatics, and in this way the lymph from every part of the body is collected and returned into the blood.

2. The Origin and Structure of Lymphatics.—The tissues of the body are built up of cells which, though lying closely applied to each other, are often separated by extremely minute spaces. These spaces are particularly plentiful in that form of tissue of which we have already spoken as connective tissue, as a result of its structural arrangement, for it is made up of bundles of fine threads or fibres which cross one another in all directions and thus form a sort of feltwork of interlacing fibres (see Fig. 28). Some of the spaces in this tissue are comparatively large and are called areolæ, whence this particular kind of connective tissue is sometimes called **areolar tissue** (see Lesson XII.). This areolar tissue is, as we have said (p. 13), present in every part of the body, and of course supports the blood-capillaries, which are thus, in reality, merely minute tubes lying imbedded in connective tissue.

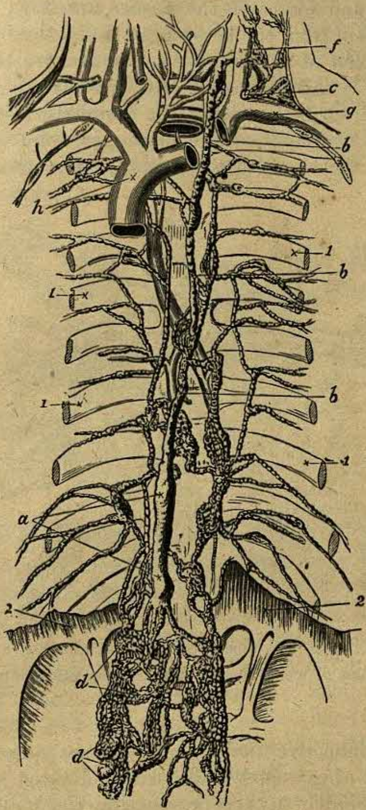

FIG. 27.—THE THORACIC DUCT.

The Thoracic Duct occupies the middle of the figure. It lies upon the spinal column, at the sides of which are seen portions of the ribs (1).

a, the receptacle of the chyle; *b*, the trunk of the thoracic duct, opening at *c* into the junction of the left jugular (*f*) and subclavian (*g*) veins as they unite into the left innominate vein, which has been cut across to show the thoracic duct running behind it; *d*, lymphatic glands placed in the lumbar regions; *h*, the superior vena cava formed by the junction of the right and left innominate veins.

The chinks and spaces of the tissues are filled with that fluid exudation from the blood-vessels and tissue elements already spoken of as lymph, and hence are themselves often called **lymph-spaces.** In these lymph-spaces we see the origin or beginning of the lymphatic system.

From the lymph-spaces the lymph passes into the lymph capillaries. These are also essentially spaces in the mesh-

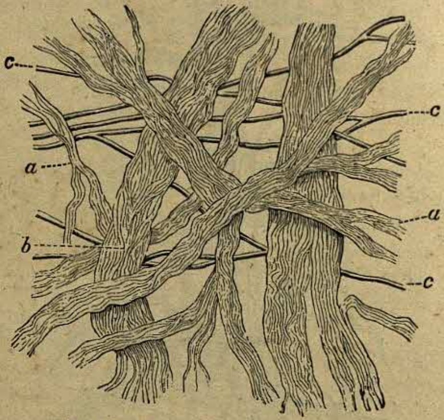

Fig. 28.—CONNECTIVE TISSUE FIBRES.

a, small bundles of white fibrous tissue; *b*, larger bundles; *c*, single elastic fibres.

work of connective tissue, but they are now lined by a single layer of extremely thin, flat, nucleated, epithelioid cells, very similar to those composing the wall of a blood capillary, but characterised by their edges being very sinuous or indented. These cells are joined to each other by their edges, the sinuosities of adjacent cells fitting into one another, so that they form a system of minute tubes, larger than blood-capillaries and wandering more irregularly.

The **lymphatic vessels** into which the lymph-capillaries pour their contents on its way towards the thoracic duct possess a structure essentially similar to that of a vein (p. 34); but they differ from a vein in that their walls are thinner, so thin as to be very transparent, are *relatively* more muscular and are more plentifully supplied with valves, whose structure, however, is the same as in the veins.

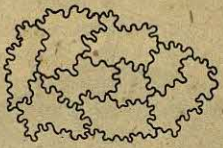

FIG. 29.—EPITHELIOID CELLS LINING, AND CHARACTERISTIC OF, THE LYMPHATICS.

The outline of the cells has been brought into view by means of nitrate of silver, which does not stain the nuclei; the latter therefore are not shown.

3. The Structure and Function of Lymphatic Glands.—Lymphatic glands occur at more or less frequent intervals along the course of the lymphatic vessels. They are of very variable size, being somewhat rounded when small and when large having more or less the shape of a bean. The afferent lymphatic vessels enter the glands by several branches on its more convex side, and emerge in diminished numbers as efferent vessels from the opposite side. Blood-vessels enter and leave the glands side by side with the efferent lymphatic vessels.

Each gland is covered externally by a **capsule** or coat of connective tissue, with which some unstriated muscle fibres are not infrequently mixed. This capsule sends projections, called **trabeculæ**, inwards and towards the centre of the gland which divide it up into compartments or **alveoli**, the compartments being very regularly arranged at the outer portion or **cortex** of the gland and

irregularly in the more central parts or **medulla** (see Fig. 30). Each alveolus is filled with a network of connective tissue, whose meshes are small and closely set in the central part of the alveolus, wider or more open when in contact with the trabeculæ. The central small meshed network is known as **adenoid tissue**,[1] is densely packed

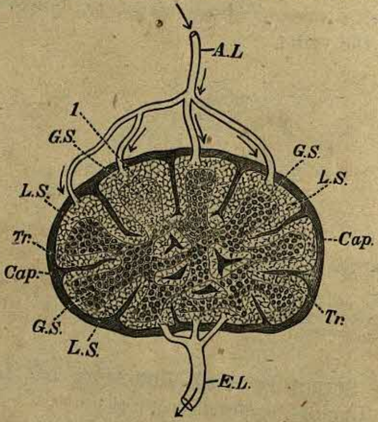

FIG. 30.—DIAGRAMMATIC REPRESENTATION OF A LYMPHATIC GLAND SEEN IN SECTION. (AFTER SHARPEY.)

Cap. capsule; *Tr.* trabeculæ; *G.S.* glandular substance; *L.S.* lymph sinus. In the alveolus marked 1. all the leucocytes are supposed to have been washed out; in the rest of the gland they are shown in the glandular substance, but washed out of the lymph-sinuses. *A.L.* afferent lymphatic; *E.L.* efferent lymphatic. The arrows show the direction in which the lymph enters and leaves the gland.

with lymph-corpuscles or **leucocytes** closely resembling the colourless corpuscles of blood (p. 100), and constitutes what is usually spoken of as the **glandular substance**. The more open-meshed network which surrounds the glandular substance and separates it from the trabeculæ is known as the **lymph-sinus** or **lymph-channel**. The meshes of the lymph-sinus, like those of the glandular substance, are crowded with leucocytes, but these are not

[1] Also often called *retiform* or *lymphoid* connective tissue. (See Lesson XII.)

very firmly fixed in this network as they are in that of the glandular substance, and may be readily washed out by shaking a thin slice of the gland in water.

The lymphatic vessels which bring lymph to the gland open directly into the channel of the lymph-sinus, and those vessels which gather up the lymph to carry it away from the gland open out of the lymph-sinuses. The arteries supplying blood to the gland pass along the trabeculæ, cross the lymph-sinus, enter the glandular substance, and break up into a network of capillaries from which the blood is collected and carried away by small veins.

The leucocytes which crowd the glandular substance present under the microscope appearances which leave no doubt that they are undergoing rapid and probably large increase in numbers. But since the size of each gland is ordinarily constant, a continual removal of the newly formed leucocytes must be taking place. This view is borne out by the observation that leucocytes are more numerous in the lymph coming from a gland than in that which flows to it. The removal takes place by a discharge of leucocytes from the glandular substance into the meshes of the neighbouring lymph-sinus, whence they are then washed away in the current of lymph which is always slowly flowing through the sinuses. In this way the lymphatic glands provide a constant supply of leucocytes which are passed ultimately into the blood and become those white or colourless corpuscles with which we shall have to deal in the next Lesson.

The lymphatic glands have another very important function. Bacteria which reach them in the lymph from some infected region are retained and destroyed in them. Otherwise these bacteria would be poured with the lymph into the blood and would infect the whole body.

4. Causes which lead to the Movements of Lymph. —Throughout the preceding description of the lymphatic system we have spoken of the lymph as flowing along a series of passages, from their origin in the tissues to the point where they become connected with the blood-vessels.

The cause of this flow is not so immediately apparent as it is in the case of the blood, for the lymphatic system possesses no central pump, such as the heart, to keep the lymph in motion.[1] In the absence then of any obviously propulsive mechanism, to what may we attribute this continual passage of lymph along the lymphatics?

The flow is in reality brought about by several causes. We may point out in the first place that some force, whose nature will be considered in the next Lesson, is at work to determine the initial exit of fluid from the blood-vessels into the lymph-spaces. This force must obviously tend to drive out the lymph already in those spaces, into and along the channels leading from them. Further, as we have seen, the blood-pressure in the large veins near the heart is very small and is certainly much less than it is in the capillaries; and since the lymphatics originate at the capillaries and discharge their contents into the great veins, this difference of pressure at the two ends of the system must tend to cause an onward flow of lymph. Here also the movements of respiration play a part, for, as will be seen when dealing with respiration, the pressure in the great veins is suddenly diminished at each inspiration and lymph is thus sucked out of the thoracic duct, no reversal of this action being possible at expiration because of the valves guarding the end of the duct. But the one great and potent cause of lymph-flow is the presence, all along the course of the lymphatics, of valves whose action is, however, only brought into play by the movements of the body. As in the veins (p. 36) so in the lymphatic vessels; when any pressure is applied to their outside the lymph is driven out of the squeezed part, and since the valves only open towards the junction of the thoracic duct with the venous system, the lymph is thereby driven along in the desired direction.

[1] The frog possesses four lymph-hearts, placed in two pairs at the upper and lower end of the backbone. Their structural arrangement is very similar to that of the blood-heart, and, being rhythmically contractile, they pump the lymph into the venous system.

LESSON III

THE BLOOD AND THE LYMPH

1. Microscopic Examination of Blood.—In order to become properly acquainted with the characters of the blood it is necessary to examine it with a microscope magnifying at least three or four hundred diameters. Provided with this instrument, a hand lens, and some slips of thick and thin glass,[1] the student will be enabled to follow the present lesson.

The most convenient mode of obtaining small quantities of blood for examination is to twist a piece of string, pretty tightly, round the middle of the last joint of the middle, or ring finger, of the left hand. The end of the finger will immediately swell a little, and become darker coloured, in consequence of the obstruction to the return of the blood in the veins caused by the ligature. When in this condition, if it be slightly pricked with a sharp clean needle (an operation which causes hardly any pain), a good-sized drop of blood will at once exude. Let it be deposited on one of the slips of thick glass, and covered lightly and gently with a piece of the thin glass, so as to spread it out evenly into a thin layer. Let a second slide receive another drop, and, to keep it from drying, let it be put under an inverted watch-glass or wine-glass, with a bit of wet blotting-paper inside. Let a third drop be dealt with in the same way, a few granules of common salt being first added to the drop.

[1] Slides and coverslips, as they are called by microscopists.

To the naked eye the layer of blood upon the first slide will appear of a pale reddish colour, and quite clear and homogeneous. But on viewing it with even a pocket lens its apparent homogeneity will disappear, and it will look like a mixture of excessively fine yellowish-red particles, like sand, or dust, with a watery, almost colourless, fluid. Immediately after the blood is drawn, the particles will appear to be scattered very evenly through the fluid, but by degrees they aggregate into minute patches, and the layer of blood becomes more or less spotty.

The "particles" are what are termed the **corpuscles** of the blood; the nearly colourless fluid in which they are suspended is the **plasma.**

The second slide may now be examined. The drop of blood will be unaltered in form, and may perhaps seem to have undergone no change. But if the slide be inclined, it will be found that the drop no longer flows; and, indeed, the slide may be inverted without the disturbance of the drop, which has become solidified, and may be removed, with the point of a penknife, as a gelatinous mass. The mass is quite soft and moist, so that this setting, the **clotting** or **coagulation,** of a drop of blood is something very different from its drying.

On the third slide, this process of clotting will be found not to have taken place, the blood remaining as fluid as it was when it left the body. The salt therefore has prevented the coagulation of the blood. Thus this very simple investigation teaches that blood is composed of a nearly colourless plasma, in which many coloured corpuscles are suspended; that it has a remarkable power of clotting; and that this clotting may be prevented by artificial means, such as the addition of salt.

If, instead of using the hand lens, the drop of blood on the first slide be placed under the microscope, the particles, or corpuscles, of the blood will be found to be bodies with very definite characters, and of two kinds, called respectively the **red corpuscles** and the **white**

or **colourless corpuscles.** The former are much more numerous than the latter, and have a yellowish-red tinge; when one of these corpuscles is seen, under a high power of the microscope, lying by itself, it seems to be hardly more than faintly yellow in colour, but when

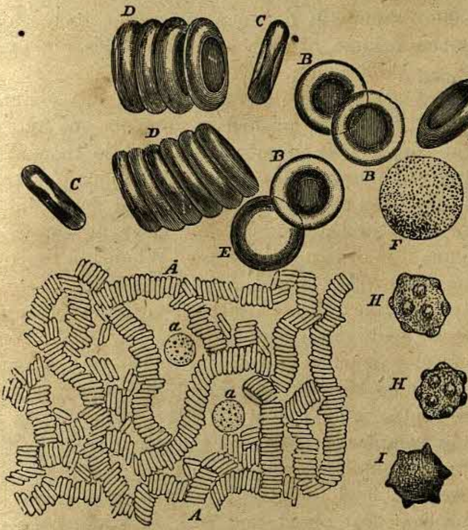

FIG. 31.—RED AND WHITE CORPUSCLES OF THE BLOOD MAGNIFIED.

A. Moderately magnified. The red corpuscles are seen lying in rouleaux; at *a* and *a* are seen two white corpuscles.

B. Red corpuscles much more highly magnified, seen in face; *C.* ditto, seen in profile; *D.* ditto, in rouleaux, rather more highly magnified; *E.* a red corpuscle swollen into a sphere by imbibition of water.

F. A white corpuscle magnified same as *B.*

H. Red corpuscles puckered or crenate all over.

I. Ditto, at the edge only.

several are seen lying one on the other, the redness becomes obvious. The white, somewhat larger than the red corpuscles, are, as their name implies, pale and devoid of colouration.

The corpuscles differ also in other and more important respects.

2. **The Red Corpuscles.**—The red corpuscles (Fig. 31) are flattened circular discs, on an average 7μ to 8μ ($\frac{1}{3200}$ of an inch) in diameter, and having about one-fourth of that thickness. It follows that rather more than 10,000,000 of them will lie on a space one inch square, and that the volume of each corpuscle does not exceed $\frac{1}{120000000000}$th of a cubic inch.

The broad faces of the discs are not flat, but somewhat concave, as if they were pushed in towards one another. Hence the corpuscle is thinner in the middle than at the edges, and when viewed under the microscope, by transmitted light, looks clear in the middle and darker at the edges, or dark in the middle and clear at the edges, according as it is or is not in focus. When, on the other hand, the discs roll over and present their edges to the eye, they look like rods. All these varieties of appearance may be made intelligible by taking a small, round, flat disc of clay or putty and squeezing the central part of the two flat sides between the thumb and finger, so as to make the centre thinner than the edges ; the disc is now more or less similar in shape to the red corpuscles, and may be turned into various positions before the eye.

In a drop of blood immediately after it is drawn, the red corpuscles float about and roll, or slide, over each other quite freely. After a short time (the length of which varies in different persons, but usually amounts to two or three minutes), they seem, as it were, to become sticky, and tend to cohere ; and this tendency increases until, at length, the great majority of them become applied face to face, so as to form long series, like rolls of coin. The end of one roll cohering with the sides of another, a network of various degrees of closeness is produced (Fig. 31, *A.*).

The corpuscles remain thus coherent for a certain length of time, but eventually separate and float freely

again. The addition of a little water, or dilute acids or saline solutions, will at once cause the rolls to break up.

It is from this running together of the corpuscles into patches of network that the change noted above in the appearances of the layer of blood, viewed with a lens, arises. So long as the corpuscles are separate, the sandy appearance lasts; but when they run together, the layer appears patchy or spotted.

The red corpuscles, rarely, if ever, all run together into rolls, some always remaining free in the meshes of the net. In contact with air, or if subjected to pressure, many of the red corpuscles become covered with little knobs, so as to look like minute mulberries—an appearance which is due to the concentrating by evaporation of the fluid in which they are floating (Fig. 31, *H*, *H*.).

The red corpuscles are very soft, flexible, and elastic bodies, so that they readily squeeze through apertures and passages narrower than their own diameters, and immediately resume their proper shapes (Fig. 25, *G*, *H*.). Examined under even a high power the red corpuscle presents no very obvious structure; when however blood is frozen and thawed one or more times, or when it is treated in certain other ways, as, for instance, by the addition of water, the colouring matter which gave each corpuscle its yellow or yellowish-red tinge is dissolved out and passes into the surrounding fluid, and all that is left of the corpuscle is a colourless framework appearing often under the microscope as a pale, hardly visible, ring. Each corpuscle in fact consists of a sort of spongy colourless framework, the **stroma**, composed of the kind of material known as **protein** and of a peculiar colouring matter, which, in the natural condition, is intimately connected with this framework, but may by appropriate means be removed from it. This colouring matter, which is of a highly complex nature, is called **hæmoglobin**, and may by proper chemical treatment be resolved into a

reddish-brown substance containing iron, called **hæmatin**, and a colourless protein substance.

Each corpuscle therefore is not to be considered as a bag or sack with a definite skin or envelope containing fluid, but rather as a sort of spongy semi-solid or semi-fluid mass, like a disc of soft jelly; and as such is capable of imbibing water and swelling up, or giving out water and shrinking according to the density of the fluid in which it may be placed. Thus, if the plasma of blood be made denser by dissolving saline substances, or sugar, in it, water is drawn from the substance of the corpuscle to the dense plasma, and the corpuscle becomes still more flattened and very often much wrinkled. On the other hand, if the plasma be diluted with water, the latter forces itself into and dilutes the substance of the corpuscle, causing the latter to swell out, and even become spherical; and, by adding dense and weak solutions alternately, the corpuscles may be made to become successively spheroidal and discoidal.

The stroma or framework constitutes but a very small part, 10 per cent., of the solid matter of which the red corpuscles are composed, the remaining 90 per cent. consisting of the colouring matter or hæmoglobin. The corpuscles may therefore be regarded as simply so many tiny masses of hæmoglobin. Now hæmoglobin, we may say at once, possesses the remarkable property of uniting in a peculiar way with considerable quantities of oxygen, and thus confers on the red corpuscles their one great characteristic of acting as the carriers of oxygen from the lungs to the tissues of all parts of the body. We have already pointed out (p. 25) the general importance of this transference of oxygen to the tissues; the details connected with the relationship of hæmoglobin to this transference may be more appropriately dealt with when we study respiration in the next Lesson.

The colouring matter of the corpuscles is further

characterised by its property of crystallising more or less readily. If a little rat's or dog's blood, from which the fibrin has been removed (see p. 111) be shaken up with a small quantity of ether, it loses its opacity and becomes quite transparent in thin layers, or as it is often called 'laky.' The transparency results from the discharge of the hæmoglobin from the stroma into the neighbouring fluid, in which it is now in solution. If the vessel con-

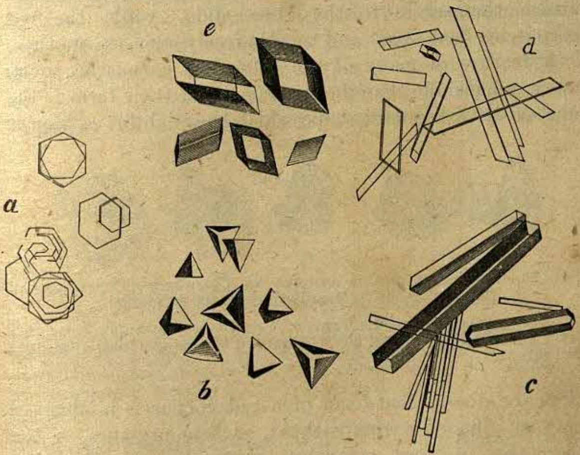

FIG. 32.—CRYSTALS OF HÆMOGLOBIN. (AFTER FUNKE.)
a, squirrel; *b*, guinea-pig; *c*, cat or dog; *d*, man; *e*, hamster.

taining the laky blood be allowed to stand on ice for some hours, a sediment usually forms at the bottom, and will be found in a successful experiment, when examined with the microscope, to consist chiefly of **blood-crystals.** The crystals differ in shape according to the animal from whose blood they were obtained; in man they have the

shape of prisms. The hæmoglobin of human blood crystallises with difficulty, but that of the guinea-pig, rat, or dog, much more readily.

3. The White Corpuscles.—The colourless corpuscles (Fig. 31, *a a*, *F.*) are larger than the red corpuscles, their average diameter being 10μ ($\frac{1}{2500}$ of an inch). They are further seen, at a glance, to differ from the red corpuscles by the irregularity of their form, and by their greater stickiness or adhesiveness, shown by their tendency to attach themselves to the glass slide, while the red corpuscles float about and tumble freely over one another.

A feature of many of the colourless corpuscles, even more remarkable than the irregularity of their form is the unceasing variation of shape which they exhibit so long as

Fig. 33.—Successive Forms assumed by Colourless Corpuscles of Human Blood. (Magnified about 600 diameters.)

The intervals between the forms *a*, *b*, *c*, *d*, was a minute; between *d* and *e* two minutes; so that the whole series of changes from *a* to *e* took five minutes.

they are alive. The form of a red corpuscle is changed only by influences from without, such as pressure, or the like; that of most colourless corpuscles is undergoing constant alteration, as the result of changes taking place in their own substance. To see these changes well, a microscope with a magnifying power of five or six hundred diameters is requisite, and some arrangement for keeping the preparation gently warmed (to 40° C.), since heat makes the movements more active; and, even then, they are so gradual that the best way to ascertain their existence is to make a drawing of a given colourless corpuscle at intervals of a minute or two. This is what has been done with the corpuscle represented in Fig. 33, in which

a represents the form of the corpuscle when first observed; *b*, its form a minute afterwards; *c*, that at the end of the second; *d*, that at the end of the third; and *e*, that at the end of the fifth minute.

Careful watching of such a colourless corpuscle, in fact, shows that every part of its surface is constantly changing —undergoing active contraction or being passively dilated by the contraction of other parts. It exhibits **contractility** in its lowest and most primitive form.

While they are thus living and active, a complete knowledge of the structure of the colourless corpuscles cannot be arrived at. Each corpuscle seems to be formed simply of a mass of the coarsely or finely granular substance called **protoplasm** in which no distinction of

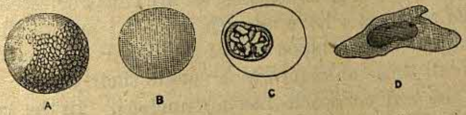

FIG. 34.—COLOURLESS CORPUSCLES OF BLOOD. (HARDY.)

A spherical and coarsely granular, the non-granular part being occupied by the nucleus; B, spherical and finely granular; C, showing nucleus after action of acetic acid; D, flattened, as the corpuscle moves, and showing the nucleus.

parts can be seen (Fig. 34, A and B). This is especially the case when the corpuscle is at rest and assumes a spheroidal shape. Sometimes, however, the corpuscle, in the course of the movements just described, spreads itself out into a very thin flat film (Fig. 34, D); and when that is the case there may be seen in its interior a body, differing in appearance from the rest of the corpuscle. Again when a drop of blood is diluted with water, still better with very dilute acetic acid, the spongy protoplasm of the white corpuscles swells up and becomes transparent, many of the granules becoming dissolved, and in this case the same body becomes visible. This internal body, which differs in nature from the rest of the

substance of the corpuscle, is called the **nucleus** (Fig. 34, C); and when the blood is treated under the microscope, with various staining fluids, such as solutions of carmine or logwood, the nucleus generally stains more deeply than the rest of the corpuscle.

Such a colourless corpuscle as has been described, with its nucleus, is what is called a **nucleated cell.** It will be observed that it lives in a free state in the plasma of the blood, and that it exhibits an independent contractility. In fact, except that it is dependent for the conditions of its existence upon the plasma, it might be compared to one of those simple organisms which are met with in stagnant water, and are called *Amœbæ*, whence the name 'amœboid' given to the movements of the colourless corpuscles of blood.

While the colourless corpuscles are thus nucleated cells, the red corpuscles have no such nucleus; and this is true not only of human blood but of the blood of all mammals, *i.e.* of all those animals which suckle their young; in all these the red corpuscle has no nucleus. In the case of birds, reptiles and fishes, however, the red corpuscles as well as the colourless are nucleated; and in the embryos[1] even of mammals the red corpuscles are at first nucleated.

Whilst all the colourless corpuscles of the blood are nucleated only about four-fifths of them have the power of amœboid movement. Those which have not this power usually, but not always, possess a cell-body which is quite clear and transparent. They are known as lymphocytes. The cell-body of the majority more usually appears to be granular from the presence in it of minute particles which, varying in size, are spoken of as 'fine' or 'coarse.' We may regard these particles as simply imbedded in the ground-substance of which the cell body is made up, and, since they are variable in size and numbers, as not essential to the structure of the corpuscle. What the real structure of the living, contractile ground-substance or protoplasm may be is still a matter of conjecture and dispute.

[1] An embryo is the rudimentary unborn young of any creature.

When the colourless corpuscles are examined chemically they are found to consist chiefly of water, and only 10–12 per cent. of solid matter. As in the case of the stroma of the red corpuscles, so here also this solid part is made up largely of **proteins** or substances closely allied to proteins. But frequently also some small amount of **fat** is found to be present, as also of a representative of that class of substances known as carbohydrates or starchy bodies, called **glycogen**, which will be dealt with later on when treating of the liver. (See Lesson V.)

The parts played by the colourless corpuscles in the animal economy are probably varied and numerous, but our knowledge of them is very imperfect. We have seen (p. 82) that under special circumstances these corpuscles may, by means of their amœboid movements, migrate in large numbers through the walls of the blood-vessels into the tissues, and it is possible that here they may in some way assist in the removal of the causes which are giving rise to the disturbance. Quite probably a similar migration is taking place on a smaller scale at all times, for some as yet obscure but possibly similar purpose. Again, by their amœboid movements the majority of colourless corpuscles can flow round small solid particles and absorb them into their cell-body; in other words they can feed on substances in the blood and thus be continually busied in keeping this fluid in a normal condition, more particularly when, as in disease, the composition of the blood is altered by the introduction of foreign matter such as bacteria, &c. Moreover it is extremely probable that the colourless corpuscles may act on the blood and on any foreign matter it may at times contain by means other than their amœboid movements; namely chemically by the discharge into the blood of substances formed within themselves. Finally there are reasons for supposing that when blood is shed, these corpuscles have something to do with starting that striking change, to which we have already alluded, known as the clotting or coagulation of blood.

4. Blood Platelets.—In addition to the red and white

corpuscles, rounded, colourless particles may, but with difficulty, be made out as existing in blood. These are known as "blood platelets." They are extremely minute, not much wider than the thickness of a red corpuscle, and usually disappear as soon as blood is removed from the body. But so little is known about them that we must not do more than simply draw attention to their existence.

5. The Origin and Fate of the Corpuscles.—The exact number of both red and colourless corpuscles present in the blood varies a good deal from time to time; and there is reason to think that both kinds of corpuscles are continually being destroyed. But since, on the whole, the average number of each kind of corpuscle is maintained during healthy life, it is evident that new corpuscles must be continually forming to take the place of those which have disappeared.

Our knowledge of the origin of the red corpuscles is somewhat indefinite; there is, however, no doubt that in the adult the chief seat of their formation lies in that marrow found in the cavities of bones which, from being very plentifully supplied with blood-vessels, is known as **red marrow**. The majority of colourless corpuscles, those which exhibit amœboid movement and granular cell-bodies also have their origin in the red marrow of the bones. There is some doubt as to whether the cells which give rise to red corpuscles in the marrow are similar to ordinary white corpuscles, or are a particular kind of cell; and the question has not as yet been definitely decided as to how the mammalian red corpuscle comes to have no nucleus, although formed in or from cells which are themselves nucleated. The lymphocytes originate in the lymphatic glands and other similar structures, are then passed along the lymphatic vessels into the blood.

Apart from what is known as to the disappearance of white corpuscles from the blood by migration through the

walls of the vessels, we cannot point with certainty to any other fate which befalls them. There is no reason for supposing that they are used up in giving rise to red corpuscles.

When we deal with the liver we shall see that the fluid (bile) which it forms or "secretes" is highly coloured, though not red. Observation and experiment both show that the substance to which the colour of bile is due is probably derived from that coloured product of the decomposition of hæmoglobin, known as hæmatin. If hæmoglobin is thus the parent substance of the colouring matter of the bile, then, since bile is formed by the liver each day in large quantities, a correspondingly large daily destruction of red corpuscles must also be taking place.

It seems probable that some destruction both of red and of colourless corpuscles takes place in the spleen.

6. **The Physical Qualities of Blood.**—The proverb that "blood is thicker than water" is literally true, as the blood is not only "thickened" by the corpuscles, of which it has been calculated that no fewer than 70,000,000,000 (eighty times the number of the human population of the globe) are contained in a cubic inch, but is rendered slightly viscid by the solid matters dissolved in the plasma. The blood is thus rendered heavier than water, its specific gravity being about 1·055. In other words, twenty cubic inches of blood have about the same weight as twenty-one cubic inches of water.

The corpuscles are heavier than the plasma, and their volume is usually somewhat less than that of the plasma. Of colourless corpuscles there are usually not more than three or four for every thousand of red corpuscles; but the proportion varies very much, increasing shortly after food is taken, and diminishing in the intervals between meals. Average blood may be regarded as consisting of $\frac{2}{3}$ plasma and $\frac{1}{3}$ corpuscles.

The blood is hot, its temperature being about 37° C. (98·6° F.).

7. **The General Composition of Blood.**—Considered

chemically, the blood is a faintly alkaline fluid, consisting of water, of solid and of gaseous matters.

The proportions of these several constituents vary according to age, sex, and condition, but the following statement holds good on the average :—

In every 100 parts of the blood there are 79 parts of water and 21 parts of dry solids ; in other words, the water and the solids of the blood stand to one another in about the same proportion as the nitrogen and the oxygen of the air. Roughly speaking, one quarter of the blood is dry, solid matter ; three quarters water. Of the 21 parts of dry solids, 12 (=$\frac{4}{7}$ths) belong to the corpuscles. The remaining 9 are about two-thirds (6·7 parts=$\frac{2}{7}$ths) proteins (substances like white of egg, coagulating by heat), and one-third (=$\frac{1}{7}$th of the whole solid matter) a mixture of saline, fatty, and carbohydrate matters and sundry products of the waste of the body, such as urea.

The total quantity of gaseous matter contained in the blood is equal to rather more than half the *volume* of the blood ; that is to say, 100 c.c. (or 100 cubic inches) of blood will contain about 60 c.c. (or 60 cubic inches) of gases. These gaseous matters are carbonic acid, oxygen, and nitrogen ; or, in other words, the same gases as those which exist in the atmosphere, but in totally different proportions ; for whereas air contains nearly three-fourths nitrogen, one-fourth oxygen, and a mere trace of carbonic acid, the average composition of the blood gases is about two-thirds or more carbonic acid, and one-third or less oxygen, the quantity of nitrogen being exceedingly small, only 1–2 c.c. in 100 c.c. of blood.

It is important to observe that blood contains much more oxygen gas than could be held in solution by pure water at the same temperature and pressure. This power of holding oxygen depends upon the red corpuscles, the oxygen thus held by them being readily given up for purposes of oxidation. The connection between the oxygen and the red corpuscles is of a peculiar nature, being a sort of loose chemical combination with one of

their constituents, and that constituent is, as we have said previously, the hæmoglobin ; for appropriate solutions of hæmoglobin behave towards oxygen almost exactly as blood does. Similarly the blood contains more carbonic acid than could be held in solution by pure water at the same temperature and pressure. But unlike the oxygen, the carbonic acid thus held by blood is not peculiarly associated with the hæmoglobin of the red corpuscles ; in fact it seems to be chiefly retained by some constituents of the plasma.

The corpuscles differ chemically from the plasma, in containing a large proportion of the fats and phosphates, all the iron, and almost all the potassium, of the blood ; while the plasma, on the other hand, contains by far the greater part of the chlorine and the sodium.

The blood of adults contains a larger proportion of solid constituents than that of children, and that of men more than that of women ; but the difference of sex is hardly at all exhibited by persons of flabby, or what is called lymphatic, constitution.

Animal diet tends to increase the quantity of the red corpuscles ; a vegetable diet and abstinence to diminish them. Bleeding exercises the same influence in a still more marked degree, the quantity of red corpuscles being diminished thereby in a much greater proportion than that of the other solid constituents of the blood.

8. The Proteins of Plasma.—By cooling or the addition of certain neutral salts the clotting of blood is retarded or even entirely prevented. The corpuscles may now be removed and the plasma obtained as a clear faintly yellow and slightly alkaline liquid composed of about 90 per cent. water and 10 per cent. of solids in solution. The solids consist chiefly of that kind of material which we have so frequently spoken of as protein. Since these proteins are typical of their class, and since proteins are without doubt the most important substances met with in the body, it will be as well to state at once what are the essential characteristics of a protein.

Proteins are, in the first place, extremely complex substances, so much so that chemists have not as yet been able to determine their constitution or assign any formula to them. Some are soluble in water, others only soluble in solutions of a neutral salt such as sodium chloride, while others are insoluble in either of the preceding solvents. When heated, those most frequently found in the body are altered or coagulated, as in the well-known change which the white of an egg, itself a typical protein, undergoes when boiled.

In the next place proteins are composed of the four elements, carbon, hydrogen, oxygen and nitrogen, with frequently a small amount of sulphur; of these the nitrogen stands out as having a supreme importance. All the tissues of the body contain nitrogen and are continually undergoing a nitrogenous waste, and the body is quite unable to make use of nitrogen for the repair of this waste except it is presented in the form of a protein. The general percentage composition of proteins is, roughly speaking, the same for all of them, and varies but slightly on either side of the following numbers:—carbon 53 parts, oxygen 22, hydrogen 7, nitrogen 16, and sulphur 1-2. In the absence of any formula this percentage composition becomes a most important characteristic.

All proteins give the three following reactions. (i) When boiled with nitric acid they turn yellow, and this yellow turns to orange on the addition of ammonia. (ii) Boiled with Millon's reagent (a mixture of the nitrates of mercury) they give a pink colour. (iii) When mixed with caustic soda and a small amount of a solution of sulphate of copper they give a violet colour. These reactions suffice for the detection of any protein in solution or as a solid.

The solids in the plasma of blood are chiefly proteins, of which there are three. The first is known as **fibrinogen** and is precipitated by the addition to plasma of 15 per cent. of sodium chloride (ordinary salt). This

result is readily attained by adding to the plasma an equal volume of a *saturated solution* of sodium chloride which contains about 30 per cent. of salt. The fibrinogen separates out from solution as a fine, flocculent, viscid precipitate. Fibrinogen is characterised by the fact that it "sets" or coagulates when heated in solution to 56° C. (132° F.). The second is called **para-globulin** and is similarly precipitated when the

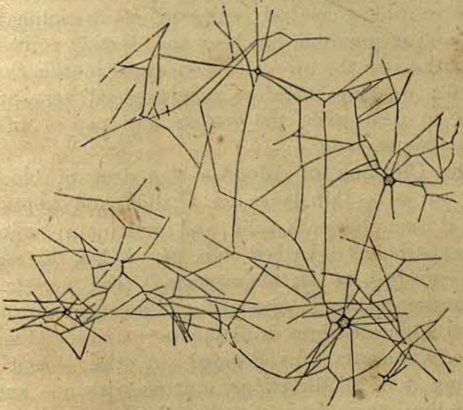

FIG. 35.—NETWORK OF FILAMENTS LEFT AFTER WASHING AWAY THE COLOURING MATTER FROM A THIN, FLAT CLOT OF BLOOD. (RANVIER.)

plasma from which the fibrinogen has been removed is subsequently saturated by the addition of as much sodium chloride as it will dissolve. It coagulates when heated in solution, at a temperature much higher than does fibrinogen, namely 75° C. (167° F.). The third is known as **serum-albumin**. It may, roughly speaking, be regarded as very like that kind of albumin with which every one is familiar in the white of an egg and while it

coagulates when heated to 75° C. (167° F.) as does paraglobulin, it differs from paraglobulin and also from fibrinogen by not being precipitated when its solution is saturated with sodium chloride.

Whilst these three proteins are characteristic of the plasma of drawn blood, it would seem that during its circulation in the body there is but one more complex protein from which these are derived.

The different precipitability of fibrinogen and paraglobulin in presence of varying amounts of sodium chloride or other "neutral" salt, such as the sulphates of sodium and magnesium, has been the starting point of all investigations on the processes concerned in the clotting of blood; we may therefore now proceed very appropriately to deal with the nature and causes of this striking phenomenon.

9. The Clotting of Blood.—If a drop of blood be spread out in a thin layer on a slide and kept from drying it soon becomes solid and gelatinous, as in the second experiment described on p. 94. When this solid is *carefully* washed, by streaming water over it very gently, the colouring matter is removed and a coarse network of extremely delicate fibres or filaments remains. (Fig. 35).

These filaments are formed in the blood and traversing it in all directions, uniting with one another and binding the corpuscles together, are the cause of the blood having become a semi-solid mass. The filaments are composed of a substance called **fibrin**; hence it is this formation of fibrin which is the cause of the solidification or clotting of the blood; but the phenomena of clotting, which are of very great importance, cannot be properly understood until the behaviour of the blood when drawn in much larger quantity than a drop has been studied.

When, by the ordinary process of opening a vein with a lancet, a quantity of blood is collected into a basin, it is at first perfectly fluid: but in a very few minutes it

becomes, through clotting, a jelly-like mass, so solid that the basin may be turned upside down without any of the blood being spilt. At first the clot is a uniform red jelly, but very soon drops of a clear yellowish watery-looking fluid make their appearance on the surface of the clot, and between it and the sides of the basin. These drops increase in number, and run together, and after a while it has become apparent that the originally uniform jelly has separated into two very different constituents—the one a clear, yellowish liquid; the other a red, semi-solid, slightly shrunken mass, which lies in the liquid. The liquid exudes from the coloured mass because the latter shrinks and so squeezes it out.

The liquid is called the **serum**; the semi-solid mass the **clot**. Now the clot obviously contains the corpuscles of the blood, bound together by some other substance; and this last, if a small part of the clot be examined microscopically, will be found to be that fibrous-looking matter, **fibrin**, which has been seen forming in the drop of blood. Thus the clot is made up of the corpuscles *plus* the fibrin of the plasma, while the serum is the plasma *minus* the fibrinous elements which it contained.

The corpuscles of the blood are slightly heavier than the plasma, and therefore, when the blood is drawn, they tend to sink very slowly towards the bottom, but as a rule clotting is complete before the corpuscles have had time to sink appreciably. When, on the other hand, the blood clots slowly, the corpuscles have so much time to sink that the upper stratum of plasma becomes quite free from red corpuscles before the fibrin forms in it; and, consequently, the uppermost layer of the clot is nearly white: it then receives the name of the *buffy coat*. This is frequently well seen in the blood of the horse, which often clots slowly, and whose corpuscles are unusually heavy.

If the blood is "whipped" with a bunch of twigs as soon as it is drawn from the body, fibrin is formed as before,

but in this case the clot is broken up as fast as it tends to be formed. Under these circumstances the fibrin collects upon the twigs, and a red fluid is left behind, consisting of the serum *plus* the red corpuscles and many of the colourless ones. The fibrin adhering to the twigs may readily be washed in a stream of water, and as thus obtained is a white, stringy, elastic and very insoluble substance. It gives, when tested, all the reactions characteristic of proteins, and is in fact itself a protein, although somewhat impure.

The clotting of the blood is hastened, retarded, or temporarily prevented by many circumstances.

(*a*) *Temperature.*—A temperature up to or slightly above 40° C. (104° F.) accelerates the clotting of the blood; a low one retards it very greatly; so much so that blood kept at a temperature close to freezing point may remain fluid for a very long time indeed.

(*b*) *The addition of neutral salts to the blood.*—Many salts, and more especially sulphate of sodium or magnesium and sodium chloride (common salt), dissolved in the blood in sufficient quantity, prevent its clotting; but clotting sets in when water is added, so as to dilute the saline mixture.

(*c*) *Contact with living or not living matter.*—Contact with not living matter promotes the clotting of the blood. Thus, blood drawn into a basin begins to clot first where it is in contact with the sides of the basin; and a wire introduced into a living vein will become coated with fibrin, although perfectly fluid blood surrounds it.

In its normal surroundings, for instance in a portion of a vein which is tied at each end, blood remains fluid for a very long time. The heart of a turtle remains alive for a lengthened period (many hours or even days) after it is extracted from the body; and, so long as it remains alive, the blood contained in it will not clot, though, if a portion of the same blood be removed from the

heart, it will clot in a few minutes. Blood taken from the body of the turtle, and kept from clotting by cold for some time, may be poured into the separated, but still living, heart, and then will not clot.

Even more remarkable is the immunity from clotting which is conferred upon blood by the salivary secretion of the leech. Blood which has been contaminated with even minute traces of this substance will remain fluid indefinitely in an open vessel.

The clotting of blood being thus due to the appearance in it of fibrin we may now consider how and why it is formed when blood is shed.

The exact nature of the changes involved in the formation of fibrin have not even yet been thoroughly worked out; but the following facts throw a good deal of light on them :—The pericardium and other serous cavities in the body, contain a clear fluid, which may be briefly described as consisting of the elements of the blood without the red blood-corpuscles. This fluid sometimes clots spontaneously, as the blood plasma would do, but very often shows no disposition to clot spontaneously, especially if it is not removed from the body until some hours after death. When the latter is the case, the fluid may nevertheless be made to clot and yield true fibrin, by adding to it a few drops of whipped blood, *i.e.* of blood which has clotted, or a little serum of blood. Now if a specimen of pericardial fluid, which has been thus observed not to clot spontaneously, but to clot readily on the addition of blood or serum, be treated with salt in the same way as described above for blood plasma, a substance will be thrown down which, at first sight, looks exactly like that thrown down from blood plasma under similar circumstances. Bnt there is a great difference, for the substance thus obtained from pericardial fluid when dissolved in water will not clot spontaneously, though its solutions may be made to clot at any time by the addition of a little serum, or whipped blood. It is clearly an

antecedent of fibrin, and indeed it was on this account that it first received the name of **fibrinogen**, or "fibrin maker," having been obtained from serous fluids before it was shown to be present in plasma. It is undoubtedly present in the substance thrown down by salt from blood plasma, but then it is mixed with other bodies; and the presence of some or other of these bodies seems to be the reason why in this case it is always converted into fibrin, and so gives a clot. Conversely the absence of this body or these bodies from pericardial fluid is the reason why pericardial fluid, or fibrinogen prepared from pericardial fluid, does not clot spontaneously.

We have previously described how this fibrinogen may be separated from plasma. If, now, the yellow fluid or serum which exudes from a blood-clot be treated with salt in a similar way (see p. 109) no fibrinogen can ever be obtained from it, while on the other hand it is found to contain both paraglobulin and serum albumin. A comparison of plasma and serum thus shows that during clotting, *i.e.* during the formation of fibrin, one constituent of the plasma, namely, fibrinogen, disappears, the other two proteins being left to appear in the serum.

Putting these facts together there can be no doubt that when blood clots the fibrin is formed out of fibrinogen. But there must also be some substance in blood after it is shed which leads to the conversion of fibrinogen into fibrin; for pericardial and other serous fluids contain fibrinogen, but do not usually clot, and purified solutions of fibrinogen never clot spontaneously. What is this substance?

If serum be precipitated with an excess of strong alcohol and after some weeks the precipitate is collected and extracted with distilled water, this watery extract contains very little solid matter, but is found to be active in causing the conversion of fibrinogen into fibrin. We do not as yet know exactly what the substance is in this extract which brings about the change of the fibrinogen,

but for reasons into which we cannot now enter, it is classed with the "ferments," of which we shall have to speak when we come to consider digestion. These ferments are characterized by their power, even when present in small quantities, of producing great changes in other bodies without themselves entering into the changes. Thus the particular ferment of which we are speaking, and which has been called "**fibrin ferment**," or "**thrombin**," produces fibrin, and yet does not itself become part of the fibrin so produced, or at all events only does so to a very slight extent.

This ferment is apparently not present in healthy blood as it circulates in the living blood-vessels, but makes its appearance when the blood is shed. We do not know exactly from what source it comes, but there are reasons for thinking that it arises from a breaking down of some kind of white corpuscle, or it may be of the blood-platelets.

This breakdown yields a substance, "*prothrombin*," which appears to be united to *salts of lime* present in the plasma, the resulting substance is thrombin. Yet one other factor is concerned in the process of coagulation, for the prothrombin and the salts of lime do not unite spontaneously. A third substance, a special kind of ferment known as a *kinase*, effects the union of the lime salts with the prothrombin. This kinase is to be found especially in injured animal tissues; therefore, while as we have already seen, blood clots very slowly in uninjured blood-vessels, it clots with great readiness when in contact with cut or bruised tissues. Clearly, in this very complicated chemical reaction, or series of reactions, we have a mechanism which is of great service to the body as it provides for the ready clotting of the blood issuing from a wound. The kinase is provided from the lips of the wound. It unites the prothrombin from the shed corpuscles with the lime salts of the plasma forming thrombin. The thrombin in turn forms fibrin out of

the fibrinogen of the plasma and the fibrin fills up the wound and assuages the bleeding.

10. The Quantity and Distribution of Blood in the Body.—The total quantity of blood contained in the body varies at different times, and the precise ascertainment of its amount is very difficult. It may probably be estimated, on the average, at not less than one-twentieth or about 5 per cent. of the weight of the body.

Its distribution may be stated in round numbers as follows:—

One quarter, in the heart, lungs and large blood vessels.

One quarter, in the liver.

One quarter, in the skeletal muscles.

One quarter, in the other organs of the body.

11. The Functions of the Blood.—The function of the blood is to supply nourishment to, and take away waste matters from, all parts of the body. All the various tissues may be said to live on the blood. From it they obtain all the matters they need, and to it they return all the waste material for which they have no longer any use. It is absolutely essential to the life of every part of the body that it should be in such relation with a current of blood, that matters can pass freely from the blood to it, and from it to the blood, by transudation through the walls of the vessels in which the blood is contained. And this vivifying influence depends upon the corpuscles of the blood. The proof of these statements lies in the following experiments:—If the vessels of a limb of a living animal be tied in such a manner as to cut off the supply of blood from the limb, without affecting it in any other way, all the symptoms of death will set in. The limb will grow pale and cold, it will lose its sensibility, and volition will no longer have power over it; it will stiffen, and eventually mortify and decompose.

But, if the ligatures be removed before the death stiffening has become thoroughly established and the

blood be allowed to flow into the limb, the stiffening speedily ceases, the temperature of the part rises, the sensibility of the skin returns, the will regains power over the muscles, and, in short, the part returns to its normal condition.

If, instead of simply allowing the blood of the animal operated upon to flow again, such blood, deprived of its fibrin by whipping, but containing its corpuscles, be artificially passed through the vessels, it will be found nearly as effectual a restorative as entire blood; while, on the other hand, the serum (which is equivalent to whipped blood without its corpuscles) has no such effect.

12. **Lymph: its Character and Composition.**—Lymph, as previously explained, is the fluid which fills the lymphatic vessels, and at the place where it is first formed is a mere overflow of fluid from the blood through the walls of the capillaries. This exudation of fluid may also be accompanied by a migration of some of the colourless corpuscles of the blood. Hence it is at once evident that lymph may, broadly speaking, be regarded as so much blood *minus* its red corpuscles.

Lymph is most easily and plentifully obtained for examination from the thoracic duct. As procured from this vessel it has the advantage of being representative of an average specimen of lymph, since it is a mixture of fluid collected from nearly all parts of the body. But the precaution must be taken of collecting the lymph from a fasting animal in order to avoid the complication due to admixture of the lymph from the body generally with certain special substances which are taken up by the lymphatics of the intestine after a meal. After a meal, the lymph from the alimentary canal differs strikingly, in one respect, as we shall see later on, from that which comes from it in the absence of food. Taking lymph, then, from the thoracic duct of a fasting animal, in which however, the lymph from the intestine still joins the lymph formed in the rest of the body, it is found

to be a transparent, faintly yellow fluid. When examined under the microscope it is seen to contain a number[1] of corpuscles, the **lymph-corpuscles** or **leucocytes**, very similar to the colourless corpuscles of blood, though perhaps on the whole rather smaller, and like the latter showing amœboid movements, especially if kept warm. These leucocytes may represent some of the white blood-corpuscles which migrated from the vessels, but by far the larger number are formed in the lymphatic glands (see p. 91).

When examined chemically lymph is found to contain the same salts as are present in plasma and in about the same amount; the total solids are, however, considerably less than in plasma,[2] and this is due to a deficiency of proteins. But the proteins present in lymph are the same in kind as the three already described as found in plasma, viz., fibrinogen, paraglobulin and serum albumin. Hence lymph clots when left to itself and yields fibrin identical with that obtained from blood, only in smaller quantities so that the clot is less firm than from blood. Some gas may also be extracted from it, but in the absence of red corpuscles the amount of oxygen it yields is scarcely appreciable; the bulk of the gas is carbonic acid and a very small amount of nitrogen.

Average lymph is therefore very similar to plasma somewhat diluted with water; but it is important to notice from what has been said above that the dilution does not affect the salts and the proteins to the same extent. Neither is the dilution the same in lymph collected from different regions of the body. Thus lymph from the arm or leg contains less, and lymph from the liver more solid matter than is present in average mixed lymph from the thoracic duct. The significance of

[1] Equal on the average to the number of white corpuscles present in blood, so that in a drop of lymph very few would be seen and often none at all.

[2] Only about 5 per cent. of its weight as compared with 8 to 10 per cent. in plasma.

these facts will become apparent when we speak of the probable mode of formation of lymph. While lymph thus differs in composition when derived from various parts of the body, it also differs when collected from the same part at different times. Usually the difference is slight, but in the case of one source it is marked and important. In a fasting animal the lymph coming from the intestines is essentially the same as average lymph; but after food has been taken, and especially if the food contains much fat, and food always contains some fat, this lymph appears to be quite white or "milky." Owing to the thinness of the walls of the lymphatics the contents are visible from their exterior, so that the vessels also appear white or milky, and hence this particular set of lymphatics is known as the **lacteals**, and the contents are called **chyle**. The only difference between chyle and the lymph ordinarily present in the lacteals is that chyle holds in suspension a large amount of fat (from 5 to 15 per cent.) in a state of extremely fine division. These minute particles of fat reflect a great deal of the light falling upon them and hence the fluid appears white. Some of the fat in chyle exists in the form of minute globules, similar to those present in milk, but the larger part is so finely divided that it can only be spoken of as "granules" and in this form is known as the *molecular basis* of chyle.

13. **The Mode of Formation of Lymph.**—In all which we have so far said respecting lymph we have spoken of it merely as an exudation of fluid from the walls of the capillaries. The word "exudation" was used purposely, as not implying more than that some of the liquid part of the blood passes out into the tissues, and certainly as not expressing any view as to the nature of the processes concerned in that passage. But now that we have dealt with the composition of lymph, and especially since we have seen that the composition varies according to the part of the body from which it flows, we may profitably con-

sider what are the causes which in the first place lead to the presence of lymph in the lymph spaces of the tissues.

Three processes suggest themselves at once as possible causes; these are **filtration**, **diffusion**, and **Osmosis.** With the first of these every one is more or less familiar, and we need say no more than that it consists in the passage of fluid and of substances in solution through a porous membrane as the result of a difference of pressure on the two sides of the membrane. Diffusion, on the other hand, is, broadly speaking, independent of the difference of pressure necessary to cause filtration. A simple experiment shows at once the essential feature of diffusion. If a small dish of parchment, similar to that in which "ices" are frequently served, be floated on water, and into the dish a solution of common table salt be placed, by chemical analysis the salt will soon be found to have passed into the water outside through the substance of the dish, even though this contains no visible holes. There will never be any appreciable difference of level between the surface of the fluid within and without the dish.

The difference between diffusion and osmosis will be understood by comparing this experiment with the following. Tie a piece of parchment paper tightly over the wide end of an ordinary "thistle tube" as used by chemists. Then fill the bulb and about one inch of the tube with a strong solution of gum acacia and fix the tube vertically, as in Fig. 36, in a beaker of water, so that the surface of the solution in the tube is *at the same level* as that of the water in the beaker. The water passes gradually through the paper into the tube so that the liquid rises in the narrow part of the tube and may ultimately stand an inch or more above the surface of that which is in the beaker. The essential difference between the two experiments lies in the fact that in the former both the water and the salt pass (diffuse) freely through the membrane, in the second the membrane is permeable to the

water but not to the gum. The gum attracts water to its side of the membrane, but does not itself traverse the membrane.

Substituting the wall of the capillaries for the paper used in the preceding experiment we have the conditions necessary for a possibly diffusive interchange between the blood on the one side of that wall and the fluid in the tissues on the other. But here we may say at once that diffusion will not account at all completely for the formation of lymph. In support of this statement it may suffice to point out that lymph contains a considerable amount of proteins, and these are characteristically non-diffusible.[1]

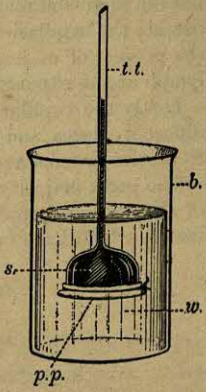

FIG. 36.—TO ILLUSTRATE A SIMPLE EXPERIMENT ON DIFFUSION.

t.t. thistle tube; *p.p.* parchment paper; *s.* solution of gum; *b.* beaker; *w.* water in beaker.

On the other hand the blood-pressure in the capillaries, though much less than in the arteries, is not inconsiderable, and is exerted against the walls of these vessels. Can we then account for the formation of lymph as the result of filtration? Here again we may at once say that the passage of fluid through the walls of the capillaries under the influence of pressure has a great deal to do with the formation of lymph. We are justified in this view by the fact, that, as a general rule, increase of blood-pressure in the capillaries leads to an increased flow of lymph from the parts they supply. But we must not conclude therefore that the process is entirely due to filtration. The process of osmosis also

[1] Substances such as the proteins of blood, also gelatin, which will not diffuse, are known as *colloids*, in contradistinction to crystalline substances or *crystalloids*, which diffuse readily.

enters largely into the cause of the flow of lymph. Speaking broadly lymph flows much more freely from organs which are in activity than from those which are at rest. The immediate result of this activity is the production of carbonic acid and more complicated substances. The carbonic acid no doubt diffuses rapidly into the blood but the more complicated bodies accumulate in the lymph outside the capillaries and attract water from the blood by the process of osmosis, thus increasing the volume of the lymph at the expense of that of the blood.

Lastly the capillary wall itself differs in character in different places and is more permeable in some places to particular substances than in others.

The great majority of the known facts about the cause of the flow of lymph can be explained by the physical factors which have been enumerated.

LESSON IV

RESPIRATION

1. The Gases of Arterial and Venous Blood.—The blood, the general nature and properties of which have been described in the preceding Lesson, is the highly complex product, not of any one organ or constituent of the body, but of all. Many of its features are doubtless given to it by its intrinsic and proper structural elements, the corpuscles; but the general character of the blood is also profoundly affected by the circumstance that every other part of the body takes something from the blood and pours something into it. The blood may be compared to a river, the nature of the contents of which is largely determined by that of the head waters, and by that of the animals which swim in it; but which is also very much affected by the soil over which it flows, by the water-weeds which cover its banks, and by affluents from distant regions; by irrigation works which are supplied from it, and by drain-pipes which flow into it.

One of the most remarkable and important of the

changes effected in the blood is that which results, in most parts of the body, from its simply passing through capillaries, or, in other words, through vessels the walls of which are thin enough to permit a free exchange between the blood and the fluids which permeate the adjacent tissues (Lesson II.).

Thus, if blood be taken from the artery which supplies a limb, it will be found to have a bright scarlet colour; while blood drawn, at the same time, from the vein of the limb, will be of a dark purplish hue. And as this contrast is met with in the contents of the arteries and veins in general (except the pulmonary artery and veins), the scarlet blood is commonly known as **arterial** and the dark blood as **venous.**

This conversion of arterial into venous blood takes place in most parts of the body, while life persists. Thus, if a limb be cut off and scarlet blood be forced into its arteries by a syringe, it will issue from the veins as dark blood.

When specimens of venous and of arterial blood are subjected to chemical examination, the differences presented by their solid and fluid constituents are found to be very small and inconstant. But the gaseous contents of the two kinds of blood differ widely in the proportion which the carbonic acid gas bears to the oxygen; there being a smaller quantity of oxygen and a greater quantity of carbonic acid, in venous than in arterial blood.

Every 100 volumes of blood contain about 60 volumes of gases. These may be extracted by boiling the blood in a vessel connected with the vacuum of a mercurial pump. The reduction of pressure on the surface of the blood leads to a rapid exit of the gases into the vacuum; they can now be collected and measured and their respective volumes determined. The composition of the blood-gases is thus found to be the following :—

	Arterial Blood.	Venous Blood.
Oxygen	20 vols.	8–12 vols.
Carbonic acid ...	40 ,, ...	46 ,,
Nitrogen	1–2 ,, ...	1–2 ,,

This difference in their gaseous contents is the most obvious difference between venous and arterial blood, as may be demonstrated experimentally. For if venous blood be shaken up with oxygen, or even with air, it gains oxygen, loses carbonic acid, and takes on the colour and properties of arterial blood. Similarly, if arterial blood be treated with carbonic acid so as to be thoroughly saturated with that gas, it gains carbonic acid, loses oxygen, and acquires the true properties of venous blood; though, for a reason to be mentioned below, the change does not take place so readily nor is it so complete in this case as in the former. The same result is attained, though more slowly, if the blood, in either case, be received into a bladder, and then placed in the oxygen, or carbonic acid; the thin moist animal membrane allowing the change to be effected with perfect ease, and offering no serious impediment to the passage of either gas.

Practically we may say that the most important difference between venous and arterial blood is not so much the relative quantities of carbonic acid as that the red corpuscles of venous blood have lost a good deal of oxygen, are reduced, and ready at once to take up any oxygen offered to them.

Similarly the loss of oxygen by the red corpuscles is the chief reason why the scarlet arterial blood turns of a more purple or claret colour in becoming venous. It has indeed been urged that the red corpuscles are rendered somewhat flatter by oxygen gas, while they are distended by the action of carbonic acid. Under the former circumstances they may, not improbably,

reflect the light more strongly, so as to give a more distinct colouration to the blood; while, under the latter, they may reflect less light, and, in that way, allow the blood to appear darker and duller.

This, however, can only be a small part of the whole matter; for solutions of hæmoglobin or of blood-crystals (Lesson III.), even when perfectly free from actual blood-corpuscles, change in colour from scarlet to purple, according as they gain or lose oxygen. It has already been stated (p. 98), that oxygen exists in the blood in loose combination with hæmoglobin. And further, a solution of hæmoglobin, when thus loosely combined with oxygen, has a scarlet colour, while a solution of hæmoglobin deprived of oxygen has a purplish hue. Hence arterial blood, in which the hæmoglobin is richly provided with oxygen, is naturally scarlet, while venous blood, which not only contains an excess of carbonic acid, but whose hæmoglobin also has lost a great deal of its oxygen, is purple.

The conditions under which the gases exist in blood are peculiar and important in connection with a point we shall have to discuss later on, namely *how* venous blood becomes arterial in the lungs and *how* arterial blood becomes venous in the tissues. As to the nitrogen, we may say at once that it is apparently in a state of simple solution, as though the blood were so much water. A very small part of the oxygen is similarly simply dissolved in the blood, but practically almost the whole of it is *in a state of loose chemical combination with the hæmoglobin of the red corpuscles.* The facts which prove this are simple and conclusive. In the absence of red corpuscles plasma and serum only absorb as much oxygen as does an equal quantity of water, namely about one volume per cent.; but blood, where the red corpuscles are present, may contain as much as 20 volumes per cent. of oxygen. Again,

solutions of hæmoglobin absorb oxygen as readily and largely as blood does. Finally, the oxygen is known to be loosely combined with the hæmoglobin, because when blood is subjected to a gradually increasing vacuum, the oxygen does not come off uniformly and progressively, as the vacuum is made greater, in the way it would if it were in mere solution; on the contrary it *escapes with a sudden rush after the pressure has been considerably reduced.*

The conditions under which carbonic acid exists in the blood may also be shown to be those of a loose chemical combination; but beyond this fact our knowledge is somewhat incomplete. It is known, however, that the carbonic acid is combined chiefly in some constituents of the plasma rather than with the corpuscles, and most authorities consider that the larger part is present in plasma united with sodium in the form of sodium bicarbonate, $NaHCO_3$.

2. **The Nature and Essence of Respiration.**—All the tissues, as we have seen, are continually using up oxygen. Their life in fact is dependent on a continual succession of oxidations. Hence they are greedy of oxygen, while at the same time they are continually producing carbonic acid (and other waste products). The demand for oxygen is met by a supply from the red corpuscles, and the oxygen they give up passes through the walls of the capillaries, across the lymph and so to the cells of which the tissue is composed. At the same time the carbonic acid passes across the lymph in the opposite direction, through the capillary walls and into the blood, by which it is at once whirled away into the veins. The blood therefore leaves the tissue poorer in oxygen and richer in carbonic acid than when it came to it; and this change is the change from the arterial to the venous condition. This gaseous interchange between the blood and the

tissues is frequently spoken of as the **respiration of the tissues** or **internal respiration.**

On the other hand, if we seek for the explanation of the conversion of the dark blood in the veins into the scarlet blood of the arteries, we find, 1st, that the blood remains dark in the right auricle, the right ventricle, and the pulmonary artery; 2nd, that it is scarlet not only in the aorta, but in the left ventricle, the left auricle, and the pulmonary veins.

Obviously, then, the change from venous to arterial takes place in the capillaries of the lungs, for these are the sole channels of communication between the pulmonary arteries and the pulmonary veins.

But what are the physical conditions to which the blood is exposed in the pulmonary capillaries?

These vessels are very wide, thin walled, and closely set, so as to form a network with very small meshes, which is contained in the substance of an extremely thin membrane. This membrane is in contact with the air, so that the blood in each capillary of the lung is separated from the air by only a delicate pellicle formed by its own wall and the lung membrane. Hence an exchange very readily takes place between the blood and the air; the latter gaining moisture and carbonic acid, and losing oxygen.[1]

This is the essential step in respiration. That it really takes place may be demonstrated very readily, by the experiment described in the first Lesson (p. 5), in which air expired was proved to differ from air inspired, by containing more heat, more water, more carbonic acid, and less oxygen; or, on the other hand, by putting a ligature

[1] The student must guard himself against the idea that arterial blood contains no carbonic acid, and venous blood no oxygen. In passing through the lungs venous blood loses only a part of its carbonic acid; and arterial blood, in passing through the tissues, loses only a part of its oxygen. In blood, however venous, there is in health always some oxygen; and in even the brightest arterial blood there is actually about twice as much carbonic acid as there is of oxygen. See the table on p. 125.

on the windpipe of a living animal so as to prevent air from passing into, or out of, the lungs, and then examining the contents of the heart and great vessels. The blood on both sides of the heart, and in the pulmonary veins and aorta, will then be found to be as completely venous as in the venæ cavæ and pulmonary artery.

But, though the passage of carbonic acid (and hot watery vapour) out of the blood and of oxygen into it is the essence of the respiratory process—and thus a membrane with blood on one side, and air on the other, is all that is absolutely necessary to effect the purification of the blood—yet the accumulation of carbonic acid is so rapid, and the need for oxygen so incessant, in all parts of the human body, that the former could not be cleared away, nor the latter supplied, with adequate rapidity, without the aid of extensive and complicated accessory machinery—the arrangement and working of which must next be carefully studied.

3. **The Organs of Respiration.**—The back of the mouth or **pharynx** communicates by two channels with the external air (see Fig. 37, *g.f.e.*). One of these is formed by the nasal passages, which cannot be closed by any muscular apparatus of their own; the other is presented by the mouth, which can be shut or opened at will.

Immediately behind the tongue, at the lower and front part of the pharynx, is an aperture—the **glottis** (Fig. 38, *Gl*)—capable of being closed by a sort of lid—the **epiglottis** (Fig. 37, *e.*)—or by the shutting together of its side boundaries, formed by the so-called **vocal cords**. The glottis opens into a chamber with cartilaginous walls —the **larynx**; and leading from the larynx downwards along the front part of the throat, where it may be very readily felt, is the **trachea**, or windpipe (Fig. 37, *c*, Fig. 38, *Tr.*).

If the trachea be handled through the skin, it will be found to be firm and resisting. Its walls are, in fact,

strengthened by a series of cartilaginous hoops, which hoops are incomplete behind, their ends being united

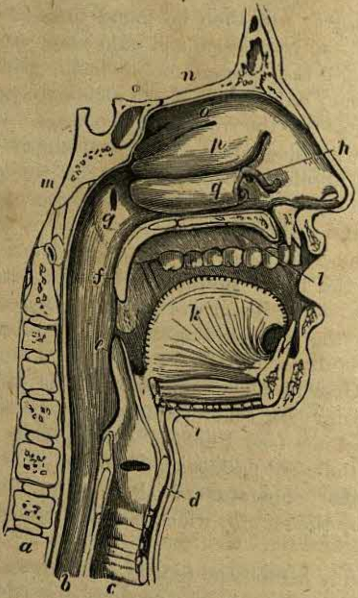

FIG. 37.—A SECTION OF THE MOUTH AND NOSE TAKEN VERTICALLY, A LITTLE TO THE LEFT OF THE MIDDLE LINE.

a, the vertebral column; *b*, the gullet; *c*, the wind-pipe; *d*, the thyroid cartilage of the larynx; *e*, the epiglottis; *f*, the uvula; *g*, the opening of the left Eustachian tube; *h*, the opening of the left lachrymal duct; *i*, the hyoid bone; *k*, the tongue; *l*, the hard palate; *m*, *n*, the base of the skull; *o*, *p*, *q*, the superior, middle, and inferior turbinal bones. The letters *g*, *f*, *e*, are placed in the pharynx.

only by muscle and membrane, where the trachea comes into contact with the *œsophagus*, or gullet. The trachea passes into the thorax, and there divides into two branches,

a right and a left, which are termed the **bronchi** (Fig. 38, *Br.*). Each bronchus enters the lung of its own side, and then breaks up into a great number of smaller branches, which are called the **bronchioles** or **bronchial tubes.** As these diminish in size, the cartilages, which are continued all through the bronchi and their

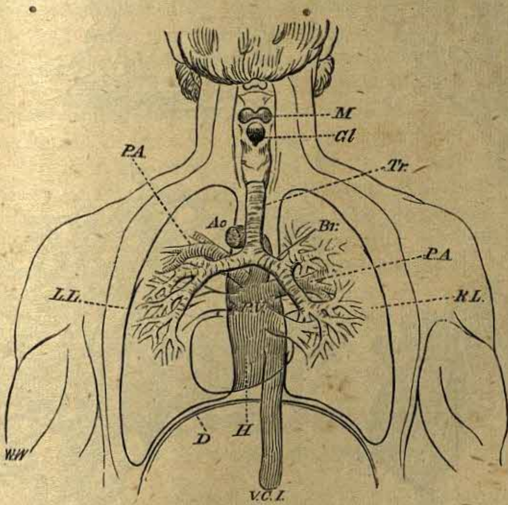

FIG. 38.—BACK VIEW OF THE NECK AND THORAX OF A HUMAN SUBJECT FROM WHICH THE VERTEBRAL COLUMN AND WHOLE POSTERIOR WALL OF THE CHEST ARE SUPPOSED TO BE REMOVED.

M. mouth; *Gl.* glottis; *Tr.* trachea; *L.L.* left lung; *R.L.* right lung; *Br.* bronchus; *P.A.* pulmonary artery; *P.V.* pulmonary veins; *Ao.* aorta; *D.* diaphragm; *H.* heart; *V.C.I.* vena cava inferior.

large ramifications, become smaller and more scattered and eventually disappear, so that the walls of the smallest bronchial tubes are entirely muscular or membranous. Thus while the trachea and bronchi are kept permanently open and pervious to air by their cartilages, the smaller

bronchial tubes may be almost closed by the contraction of their muscular walls.

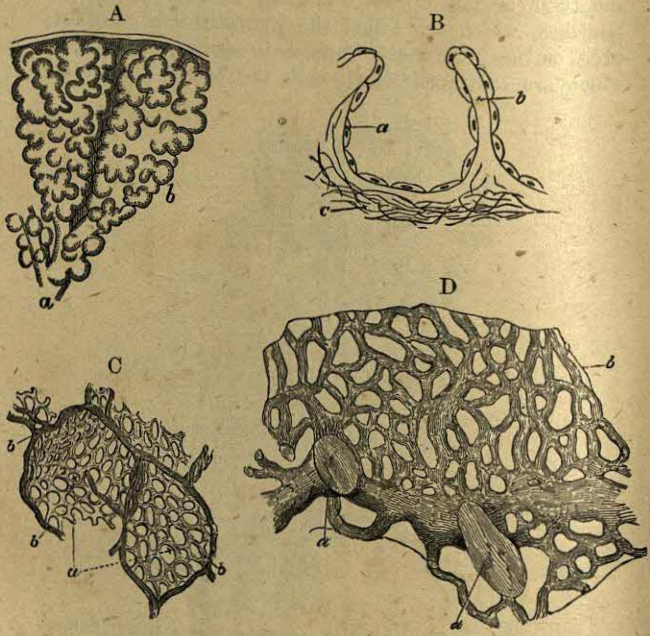

FIG. 39.

A. Two infundibula (*b*) with the ultimate bronchial tube (*a*) which opens into them. (Magnified 20 diameters.)

B. Diagrammatic view of an air-cell of A seen in action; *a*, epithelium; *b*, partition between two adjacent cells, in the thickness of which the capillaries run; *c*, fibres of elastic tissue.

C. Portion of injected lung magnified: *a*, the capillaries spread over the walls of two adjacent air-cells; *b*, small branches of arteries and veins.

D. Portion still more highly magnified.

Each finer bronchiole ends at length in an elongated dilatation about $\frac{1}{30}$ of an inch in diameter on the average and known as an **infundibulum** (Fig. 39, A. b). The wall

of an infundibulum sends flattened projections into its interior and thus forms a series of thin partitions by which the cavity of the infundibulum is divided up into a large number of little sacs or chambers. These sacs are the **alveoli** or **air-cells**.

The very thin walls (Fig. 39, B *b*) which separate these alveoli are supported by much delicate and *highly elastic tissue*, and carry the wide and close-set capillaries into which the ultimate ramifications of the pulmonary artery pour its blood (Fig. 39, C, D). Thus, the blood contained in these capillaries is exposed on both sides to the air—being separated from the alveolus on either hand only by the very delicate pellicle which forms the wall of the capillary, and the lining of the alveolus. The partitions between the alveoli are covered with extremely thin flattened cells, which may be easily seen in the lung of a young animal but are reduced to almost nothing in the lung of an adult.

The infundibula are bound together in groups by connective tissue to form larger masses termed **lobules**. These lobules are similarly bound together in groups to form **lobes** and the several lobes are united to form a lung. The blood-vessels, nerves and lymphatics of each lung are carried by the connective tissue which binds the whole together.

The trachea is essentially a tube whose wall is strengthened and whose bore is kept open by C-shaped hoops or rings of cartilage. These hoops lie imbedded in fibrous connective tissue in the outer part of the wall, in which also there is a certain amount of unstriated muscular tissue, running chiefly across the space between the ends of each cartilaginous hoop. The inner surface of the tube is lined with a **mucous membrane**.[1] This consists of

[1] This name is applied generally to the membranes lining those internal passages of the body which communicate with its surface, such as the respiratory passages, the alimentary canal, and the bladder. Mucous membranes become continuous with the skin at the edge of the opening on the surface. They derive their name from the fact that they

an epithelium of **ciliated cells**, interspersed with **mucous cells**; these lie on a distinct basement membrane and below this is a small amount of lymphoid and elastic tissue. (See Lesson XII.) Between the mucous membrane and the outer layer which carries the hoops of cartilage, there is a certain amount of areolar connective

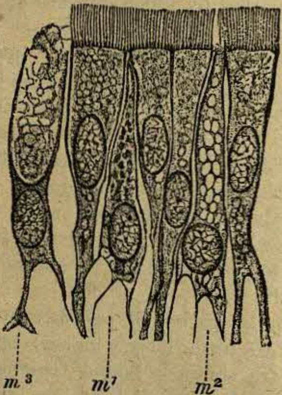

FIG. 40.—CILIATED EPITHELIUM CELLS FROM THE TRACHEA OF THE RABBIT, HIGHLY MAGNIFIED. (SCHÄFER.)

m^1, m^2, m^3, mucus-secreting cells lying between the ciliated cells and seen in various stages of mucin-formation.

tissue (p. 86), in which some small mucous glands are imbedded; this constitutes the submucous layer. The ciliated cells are elongated columnar cells with a large and distinct nucleus. During life the cilia vibrate incessantly backwards and forwards, but work on the whole in such a way as to sweep both liquid (mucus) and solid particles outwards or towards the mouth. (See also Lesson VII.) The mucous and ciliated cells extend from the trachea into the smallest branches of the bronchi.

are covered with a viscid secretion called **mucus**, whose characteristic constituent, **mucin**, is secreted by special mucous cells or by small mucous glands, imbedded in or lying beneath the membrane.

No conditions could be more favourable to a ready exchange between the gaseous contents of the blood and those of the air in the alveoli than the arrangements which obtain in the pulmonary capillaries; and, thus far, the structure of the lung fully enables us to understand how it is that the large quantity of blood poured through the pulmonary circulation becomes exposed in very thin streams, over a large surface, to the air. But the only result of this arrangement would be, that the pulmonary air would very speedily lose all its oxygen, and become completely saturated with carbonic acid, if special provision were not made for its being incessantly renewed. The renewal is brought about by the working of certain structural and mechanical arrangements which must now be described in detail.

4. **The Thorax and Lungs.**—The lungs (and heart) are enclosed in what is practically an air-tight box, whose walls are movable. This box is the thorax. In shape it is conical, with the small end turned upwards, the back of the box being formed by the spinal column, the sides by the ribs, the front by the sternum or breast-bone, the bottom by the diaphragm, and the top by the root of the neck (Fig. 38).

The two lungs occupy almost all the cavity of this box which is not taken up by the heart (Fig. 41). Each is enclosed in its serous membrane, the **pleura**, a double bag (very similar to the pericardium, the chief difference being that the outer bag of each pleura is, over the greater part of its extent, quite firmly adherent to the walls of the chest and the diaphragm, while the outer bag of the pericardium is for the most part loose), the inner bag closely covering the lung and the outer forming a lining to the cavity of the chest[1] (Fig. 42, pl.). So long as the walls of the thorax are entire, the cavity of each

[1] There is a small amount of fluid between the two surfaces of the pleura, to facilitate their rubbing easily against one another. This "serous" fluid is in reality, as is pericardial fluid, a form of lymph.

pleura is practically obliterated, that layer of the pleura which covers the lung being in close contact with that which lines the wall of the chest; but if a small opening

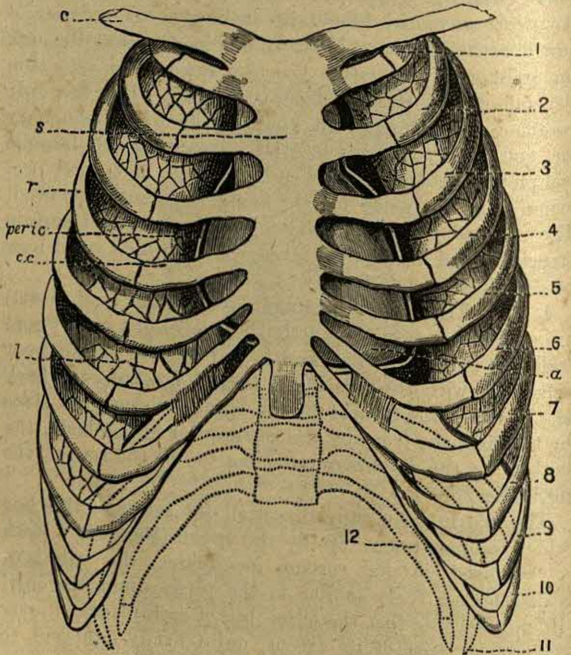

FIG. 41.—DIAGRAM OF THE THORAX SHOWING THE POSITION OF THE HEART AND LUNGS.

1-12, ribs; 11-12, floating ribs; *s*, sternum; *r*, rib; *c.c*, costal cartilages; *c*, clavicle; *l*, lungs; *a*, apex of heart; *peric.* pericardium, cut edge.

be made into the pleura, the lung at once shrinks to a comparatively small size, and thus develops a great cavity between the two layers of the pleura. If a pipe be now fitted into the bronchus, and air blown through it, the

lung is very readily distended to its full size; but, on being left to itself, it collapses, the air being driven out again with some force. The abundant elastic tissues of the walls of the air-cells are, in fact, so disposed as to be greatly stretched when the lungs are full; and when the cause of the distension is removed, this elasticity comes into play and drives the greater part of the air out again.

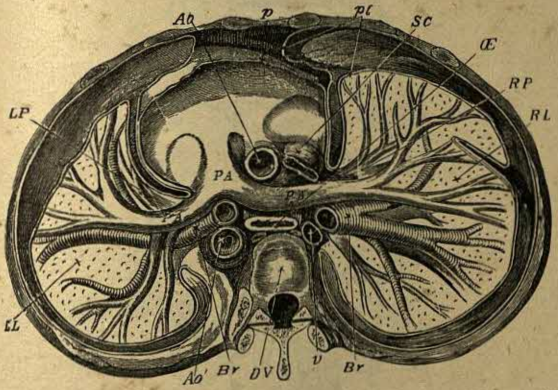

FIG. 42.—TRANSVERSE SECTION OF THE CHEST, WITH THE HEART AND LUNGS IN PLACE. (A little diagrammatic.)

D.V. dorsal vertebra, or joint of the backbone; *Ao. Ao'.* aorta, the top of its arch being cut away in this section; *S.C.* superior vena cava; *P.A.* pulmonary artery, divided into a branch for each lung; *L.P. R.P.* left and right pulmonary veins; *Br.* bronchi; *R.L. L.L.* right and left lungs; *Œ.* the gullet or œsophagus; *p.* outer bag of pericardium; *pl.* the two layers of pleura; *v.* azygos vein.

The lungs are kept distended in the dead subject, so long as the walls of the chest are entire, by the pressure of the atmosphere acting down the trachea, bronchi and bronchioles upon the inner surfaces of the walls of the alveoli. For though the elastic tissue is all the while pulling, as it were, at the layer of pleura which covers the lung, and attempting to separate it from that which lines

the chest, it cannot produce such a separation without developing a vacuum between these two layers. To effect this, the elastic tissue must pull with a force greater than that of the external air (or fifteen pounds to the square inch), an effort far beyond its powers, which do not equal

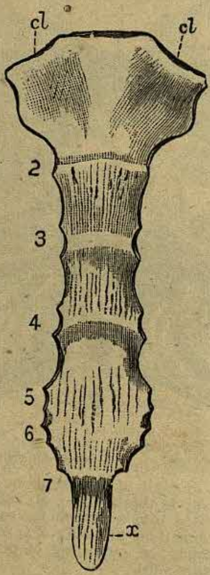

FIG. 43.—STERNUM VIEWED FROM THE FRONT.

1-7, points of attachment of first seven ribs; *cl.* points of attachments of clavicles (collar-bones); *x*, lower projecting end of sternum.

one-fourth of a pound on the square inch. But the moment a hole is made in the pleura, the air enters into its cavity, the atmospheric pressure inside the lung is equalised by that outside it, and the elastic tissue, freed

from its opponent, exerts its full power on the lung and it collapses.

5. **The Movements of Respiration.**—The hinder ends of the ribs are attached to the vertebral column so as to

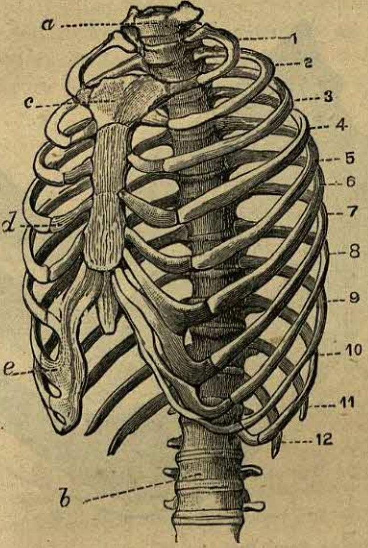

FIG. 44.—THE BONY WALLS OF THE THORAX.

a, *b*, vertebral column; 1-12, ribs; *c*, sternum; *d* costal cartilages; *e*, united cartilages of lower true ribs.

be freely movable upon it. The front ends of the first ten pairs of ribs are connected either directly (first seven ribs), or indirectly (next three ribs), by the costal cartilages to the sternum, the connection being therefore flexible (Figs. 41, 44, 45). When left to themselves the ribs take a position which is inclined obliquely downwards and forwards.

Two sets of muscles, called **intercostals**, pass between the successive pairs of ribs on each side. The outer set, called **external intercostals** (Fig. 45, *A*), run from the rib above, obliquely downwards and forwards, to the

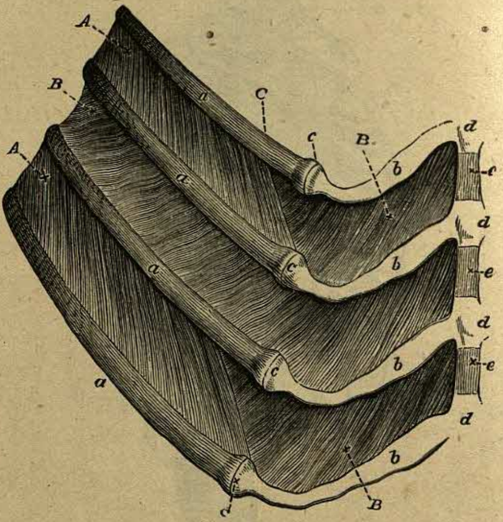

FIG. 45.—VIEW OF FOUR RIBS OF THE DOG WITH THE INTERCOSTAL MUSCLES.

a, the bony rib; *b*, the cartilage; *c*, the junction of bone and cartilage; *d*, unossified, *e*, ossified, portions of the sternum. *A*, external intercostal muscle; *B*, internal intercostal muscle. In the middle interspace, the external intercostal has been removed to show the internal intercostal beneath it.

rib below. The other set, **internal intercostals** (Fig. 45, *B*), cross these in direction, passing from the rib above, downwards and backwards, to the rib below.

The action of these muscles is somewhat puzzling at first, but is readily understood if the fact that *when a*

muscle contracts, it tends to shorten the distance between its two ends be borne in mind. Let a and b in Fig. 46, A, be two parallel bars, representing two consecutive ribs, movable by their ends upon the upright c, which may be regarded as the vertebral column at the back of the apparatus; then a line directed from x to y will be inclined downwards and forwards, and one from w to z will be directed downwards and backwards. Now it is obvious from the figure that the distance between x and y is

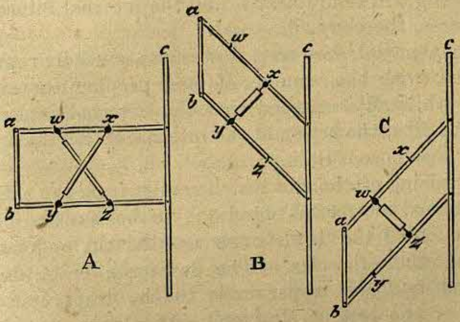

FIG. 46.—DIAGRAM OF MODELS ILLUSTRATING THE ACTION OF THE EXTERNAL AND INTERNAL INTERCOSTAL MUSCLES.
B, inspiratory elevation; C, expiratory depression.

shorter in B than in A and much shorter than in C; hence when $x\ y$ is shortened the bars will be pulled up from the position C or A to or towards the position B. Conversely, the shortening of $w\ z$ will tend to pull the bars down from the position B or the position A to or towards the position C.

If the simple apparatus just described be made of wood, hooks being placed at the points $x\ y$, and $w\ z$; and an elastic band be provided with eyes which can be readily put on to or taken off these hooks; it will be found that

the band being so short as to be put on the stretch when hooked on to either x y, or w z, with the bars in the horizontal position, A, the elasticity of the band, when hooked on to x and y, will bring them up as shown in B; while, if hooked on to w and z, it will bring them down as shown in C.

Substitute the contractility of the external and internal intercostal muscles for the shortening of the band, in virtue of its elasticity, and the model will exemplify the action of these muscles; the external intercostals in shortening will tend to raise, and the internal intercostals to depress, the bony ribs.

Such a model, however, does not accurately represent the ribs, with their numerous and peculiar curves, and hence, while all are agreed that the external intercostals raise the ribs, the action of the internal intercostals is not by any means so certain.

The raising of the ribs which results from the action of the external intercostal muscles is further assisted by the contraction of the **levatores costarum** and perhaps certain other muscles. The levatores costarum are attached by their upper ends to the transverse processes of the last cervical and first eleven dorsal vertebræ, and each muscle is fastened by its lower end to the rib next below the vertebra from which the muscle itself springs. These muscles must also by their contraction raise the ribs.

By means of these several muscles the ribs can be raised from their naturally downward-slanting position into one more nearly horizontal. When this takes place, the front ends of the ribs must move not only upwards but forwards, and must therefore thrust the sternum slightly outwards, or away from the vertebral column. By this movement the size of the thorax is of course *increased from back to front*, an increase which may be easily felt by placing one hand on the back and one on the chest of a

person who is breathing. Again, when the ribs are raised, each rib must evidently, by its upward motion, tend to occupy the position previously held by the rib next above it; but the arched curve of each rib increases in size from the first to the seventh pair of ribs, so that this upward movement makes a rib with a larger arch take the place of one with a smaller curve. This must clearly result in an *increase in width of the thorax from side to side*, an increase which may, as before, be readily felt by placing the hands on the opposite sides of the chest.

The floor of the thorax is formed by the diaphragm, a great partition situated between the thorax and the abdomen, and always concave to the latter and convex to the former (Fig. 1, *D*). From its middle, which is tendinous, muscular fibres extend downwards and outwards to the ribs, and two, especially strong masses, which are called the *pillars of the diaphragm*, to the spinal column (Fig. 47). When these muscular fibres contract, therefore, they tend to make the diaphragm flatter, and to increase the capacity of the thorax at the expense of that of the abdomen, by pulling down the bottom of the thoracic box (Fig. 48, *A*), or in other words when the diaphragm is flattened, the size of the thorax is *increased from above downwards*.

By means then of the movements of the ribs and of the diaphragm the size of the thorax may be increased in all its dimensions. Let us now consider what must happen to the lungs when the thorax becomes larger. The lungs, as we have said (p. 137), are kept distended by the pressure of the atmosphere acting down the trachea and keeping the outer walls of each lung firmly pressed against the inner wall of the chest. This being so, if the wall of the thorax tends to move away from the wall of the lung, as it must do when the thorax is enlarged, then the wall of the lung must follow the wall of the thorax, air rushing in through the trachea to increase the distension of the

elastic lungs to the required extent, and to prevent the formation of any vacuum between the two pleuræ. This drawing of air into the lungs constitutes an **inspiration.**

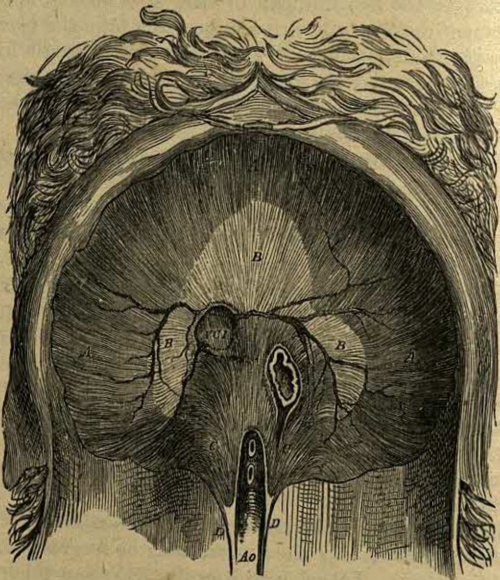

FIG. 47.—THE DIAPHRAGM OF A DOG VIEWED FROM THE LOWER OR ABDOMINAL SIDE.

V.C.I, the vena cava inferior; *O*, the œsophagus; *Ao*. the aorta; the broad white tendinous middle (*B.B.B*) is easily distinguished from the radiating muscular fibres (*A.A.A*) which pass down to the ribs and into the pillars (*C. D*) in front of the vertebræ.

At the end of each inspiration the diaphragm ceases to contract and the external intercostal muscles relax. So much of the elasticity of the lungs as was called into play by the contraction of the diaphragm and the

raising of the ribs now comes into action; air is driven out of the lungs and the diaphragm rises to its former position (Fig. 48, *B*), being partly also pushed up by the abdominal viscera which were pushed down when the diaphragm contracted. At the same time gravity acting on the ribs tends to lower them, and this is assisted by the elastic recoil of the lungs and of the tissues of the chest wall which had been put on the stretch during inspiration, and possibly also by the contraction of the internal intercostal muscles. By these means air is driven out of the lungs, the forcing out of the air constituting an **expiration**, which taken together with an inspiration makes up **respiration.**

Thus it appears that we may have either *diaphragmatic respiration*, or *costal respiration*. As a general rule, however, the two forms of respiration coincide and aid one another, the contraction of the diaphragm taking place at the same time with that of the external intercostals, and its relaxation with their relaxation.

In ordinary quiet respiration, inspiration is an active process depending on the contraction of muscles; expiration, on the other hand, is rather due to a passive recoil of elastic structures which had been previously put on the stretch. But at times, as when taking violent exercise, the respiration becomes more forcible or, as it is called, "laboured." In this case many accessory muscles come into play to assist during inspiration in raising the ribs and sternum; being chiefly muscles stretched between the ribs and parts of the vertebral column—above them at the back, and between the neck and the sternum in front. At the same time expiration, from being passive now also becomes an active process, chiefly by the contraction of certain muscles which connect the ribs and breast-bone with the pelvis, and form the front and side walls of the abdomen, the abdominal muscles. They assist expiration in two ways: first, directly, by pulling down the ribs; and next, indirectly, by pressing the

viscera of the abdomen upwards against the under surface of the diaphragm, and so driving the floor of the thorax upwards.

It is for this reason that, whenever a violent expiratory effort is made, the walls of the abdomen are obviously flattened and driven towards the spine, the body being at the same time bent forwards.

In taking a deep inspiration, on the other hand, the walls of the abdomen are relaxed and become convex, the viscera being driven against them by the descent of the diaphragm—the spine is straightened, the head thrown back, and the shoulders outwards, so as to afford the greatest mechanical advantage to all the muscles which can elevate the ribs.

It is a remarkable circumstance that the mechanism of respiration is somewhat different in the two sexes. In men, the diaphragm takes the larger share in the process, the upper ribs moving comparatively little; in women, the reverse is the case, the respiratory act being more largely the result of the movement of the ribs.

Sighing is a deep and prolonged inspiration. "*Sniffing*" is a more rapid inspiratory act, in which the mouth is kept shut, and the air made to pass through the nose.

Hiccough is the result of a sudden inspiration, due to a contraction of the diaphragm, during which the glottis is suddenly closed and the column of air, striking on the closed glottis, gives rise to the well-known and characteristic sound.

Coughing is a violent expiratory act. A deep inspiration being first taken, the glottis is closed and then burst open by the violent compression of the air contained in the lungs by the contraction of the expiratory muscles, the diaphragm being relaxed and the air driven through the mouth. In *sneezing*, on the contrary, the cavity of the mouth being shut off from the pharynx by the approximation of the soft palate and the base of the tongue, the air is forced through the nasal passages.

It thus appears that the thorax, the lungs, and the trachea constitute a sort of bellows without a valve, in which the thorax and the lungs represent the body of the bellows, while the trachea is the pipe; and the effect of the respiratory movements is just the same as that of

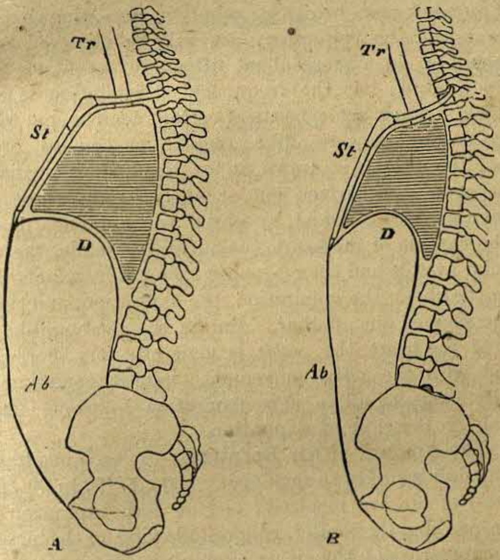

Fig. 48.—Diagrammatic Sections of the Body in

A, inspiration; *B*, expiration; *Tr*, trachea; *St*, sternum; *D*, diaphragm; *Ab*, abdominal walls. The shading roughly indicates the stationary air.

the approximation and separation of the handles of the bellows, which drive out and draw in the air through the pipe. There is, however, one difference between the bellows and the respiratory apparatus, of great importance in the theory of respiration, though frequently overlooked; and that is, that the sides of the bellows can be brought

close together so as to force out all, or nearly all, the air which they contain ; while the walls of the chest, when approximated as much as possible, still inclose a very considerable cavity (Fig. 48, *B*) ; so that, even after the most violent expiratory effort, a very large quantity of air is left in the lungs.

If an adult man, breathing calmly in the sitting position, be watched, the respiratory act will be observed to be repeated on an average about fifteen to seventeen times every minute ; but the frequency of repetition is very variable. Each act consists of certain components which succeed one another in a regular rhythmical order. First, the breath is drawn in or inspired, immediately afterwards it is driven out or expired ; and these successive acts are followed by a brief pause. Thus, just as in the rhythm of the heart, the auricular systole, the ventricular systole and then a pause follow in regular order ; so in the chest, the inspiration, the expiration, and then a pause succeed one another. But in the chest, unlike the case of the heart, the pause is generally very short compared with the active movement ; indeed, sometimes it hardly exists at all, a new inspiration following immediately on the close of expiration.

6. **The Amount of Air Respired.**—At each inspiration of an adult well-grown man about 500 c.c. (20 to 30 cubic inches) of air are inspired ; and at each expiration the same, or a slightly smaller, volume (allowing for the increase of temperature of the air so expired) is given out of the body. To this the name of **tidal air** has been conveniently given.

The amount of air which, as already pointed out, cannot be got rid of by even the most violent expiratory effort and is called **Residual air**, is, on the average, about 1,500 c.c. (from 75 to 100 cubic inches).

About as much more in addition to this remains in the chest after an ordinary expiration, and is called **Supplemental air.**

Thus it follows that, after an ordinary inspiration, 1,500+1,500+500=3,500 c.c. (100+100+30=230 cubic inches) may be contained in the lungs. By taking the deepest possible inspiration, another 1,500 c.c. (100 cubic inches), called **Complemental air**, may be added.

The sum of the supplemental, tidal, and complemental air amounts to about 3,500 to 4,000 c.c. (230 to 250 cubic inches), and is a measure of what is known as the *respiratory* or *vital capacity*. It varies according to a person's height, weight, and age.

It results from these data that the lungs, after an ordinary inspiration, contain about 3,500 c.c. (230 cubic inches) of air, and that only about one-seventh to one-eighth of this amount is breathed out and taken in again at the next inspiration. Apart from the circumstance, then, that the fresh air inspired has to fill the cavities of the hinder part of the mouth, and the trachea, and the bronchi, if the lungs were mere bags fixed to the end of the bronchi, the inspired air would descend so far only as to occupy that one-fourteenth to one-sixteenth part of each bag which was nearest to the bronchi, whence it would be driven out again at the next expiration. But as the bronchi branch out into a prodigious number of bronchial tubes, the inspired air can only penetrate for a certain distance along these, and can never reach the air-cells at all.

Thus the residual and supplemental air taken together are, under ordinary circumstances, *stationary*—that is to say, the air comprehended under these names merely shifts its outer limit in the bronchial tubes, as the chest dilates and contracts, without leaving the lungs, and is hence called **stationary air**; the *tidal* air, alone, being that which leaves the lungs and is renewed in ordinary respiration.

It is obvious, therefore, that the business of respiration is essentially transacted by the stationary air, which plays the part of a middleman between the two parties—the

blood and the fresh tidal air—who desire to exchange their commodities, carbonic acid for oxygen, and oxygen for carbonic acid.

Now there is nothing interposed between the fresh tidal air and the stationary air; they are gaseous fluids, in complete contact and continuity, and hence the exchange between them must take place according to the ordinary laws of gaseous diffusion.

Thus, the stationary air in the air-cells, or, as it is frequently called, **Alveolar Air**, gives up oxygen to the blood, and takes carbonic acid from it, though the exact mode in which the change is effected is not thoroughly understood. By this process it becomes loaded with carbonic acid, and deficient in oxygen. There is very much greater excess of the one, and deficiency of the other, than is exhibited by inspired air, seeing that the latter acquires its composition by diffusion in the short space of time (four or five seconds) during which it is in contact with the alveolar air.

Dry alveolar air contains in each 100 volumes—

Oxygen	Nitrogen	Carbonic Acid
14·5	80	5·5

7. The Changes of Air in Respiration.—Expired air differs from the air inspired in the following particulars.

(i) Speaking generally, whatever be the temperature of the external air, that expired tends to be nearly as hot as the blood, or has a temperature of about 37° C. (98·6° F.).

(ii) However dry the external air may be, that expired is nearly, or quite, saturated with watery vapour. This vapour is not derived from the stationary air, but from the walls of the outer air passages, so that the inspired air is practically saturated with aqueous vapour before it reaches the bronchi.

(iii) While ordinary inspired air contains in 100 volumes—

Oxygen	Nitrogen	Carbonic Acid
20·96	79·00	·04

the composition of expired air is on the average in 100 volumes—

Oxygen	Nitrogen	Carbonic Acid
16·50	79·50	4·00

Thus, speaking roughly, air which has been breathed once has gained 4 per cent. of carbonic acid and lost rather more than 4 per cent. of oxygen, the quantity of nitrogen being practically unchanged.

(iv) Expired air contains, in addition, small quantities of "animal matter" or organic impurities of a highly decomposable kind. Nothing is known of their nature, but they are probably the chief cause, why air which has been breathed once is extremely unwholesome if breathed a second time; hence they are of great importance in connection with ventilation (see p. 168).

(v) The volume of the tidal air is but little altered by being breathed, because the two parts of oxygen in the carbonic acid (CO_2) occupy the same volume as the carbonic acid itself, or in other words the volume of the carbonic acid is equal to that of the oxygen contained in it. But as a matter of fact very close analysis of the expired air shows firstly that the volume of oxygen which disappears is slightly greater than the volume of carbonic acid which takes its place. This is because all the oxygen taken in does not gc to form carbonic acid; some of it unites with hydrogen to form water and some with other elements such as sulphur. Hence the volume of the expired air is slightly ($\frac{1}{50}$) less than that of the inspired air. In the second place careful analysis shows that the nitrogen in expired air may vary very slightly: sometimes it is a little in excess of, sometimes slightly less than, that inspired, and sometimes it remains unaltered.

8. The Amount of Waste which leaves the Lungs.— About 10,000 litres (from 350 to 400 cubic feet) of air are passed through the lungs of an adult man taking little or

no exercise, in the course of twenty-four hours, and are charged with carbonic acid, and deprived of oxygen, to the extent of about four per cent. This amounts to about 450 litres (16 cubic feet) of the one gas taken in, and of the other given out. Thus, if a man be shut up in a close room, having the form of a cube seven feet in the side, every particle of air in that room will have passed through his lungs in twenty-four hours, and a fifth of the oxygen it contained will be replaced by carbonic acid.

The quantity of carbon eliminated in the twenty-four hours is pretty nearly represented by a piece of pure charcoal weighing 225 grammes (eight ounces).

The quantity of water given off from the lungs in the twenty-four hours varies very much, but may be taken on the average as rather less than 250 c.c. (half a pint, or about nine ounces). It may fall below this amount, or increase to double or treble the quantity.

The air expired during the first half of an expiration contains less carbonic acid than that expired during the second half. Further, when the frequency of respiration is increased without altering the volume of each inspiration, though the percentage of carbonic acid in each expiration is diminished, it is not diminished in the same ratio as that in which the number of inspirations increases; and hence more carbonic acid is got rid of in a given time.

Thus, if the number of inspirations per minute is increased from fifteen to thirty, the percentage of carbonic acid evolved in the second case remains more than half of what it was in the first case, and hence the total evolution is greater.

This does not imply that there is a greater formation of carbonic acid in the tissues, but only that the carbonic acid in the blood passes more rapidly into the alveolar air and is in turn replaced by that in the tissues. Thus the

quantity of carbonic acid in the body is reduced, and indeed the whole condition is one which cannot be maintained for more than a few minutes.

The activity of the respiratory process is greatly modified by the circumstances in which the body is placed. Thus, cold greatly increases the quantity of air which is breathed, the quantity of oxygen absorbed, and of carbonic acid expelled : exercise and the taking of food have a corresponding effect.

In proportion to the weight of the body, the activity of the respiratory process is far greatest in children, and diminishes gradually with age.

The excretion of carbonic acid is greatest during the day, and gradually sinks at night, attaining its minimum about midnight, or a little after.

The quantity of oxygen which disappears in proportion to the carbonic acid given out, is greatest in carnivorous, least in herbivorous animals—greater in a man living on a flesh diet, than when the same man is feeding on vegetable matters.

9. The Nature of the Respiratory Changes in the Lungs and Tissues.—The essential difference between venous and arterial blood is, as we have previously explained, entirely dependent upon the relative amounts of the two gases, oxygen and carbonic acid, which they respectively contain. We have also pointed out where the changes from arterial to venous blood and *vice versa*, take place, and have indicated the general causes of the conversion as being an interchange between the blood and the tissues on the one hand, and between the blood and the stationary air in the lungs on the other. But we have not so far dealt with the nature of the processes involved in effecting the interchange, and to these we must now turn our attention.

A clear understanding of certain facts and principles

as to the behaviour of gases towards each other and towards liquids with which they may be in contact is essential as a preliminary.

When a gas is enclosed in a vessel, it exerts a pressure on its walls which is measured by the height of the column of mercury which it can support in a vertical tube connected with the vessel. If two gases are mixed in the vessel, each gas exerts its own pressure just as if the other gas were not present; the total pressure of the two gases is therefore *equal to the sum of their separate pressures.* The pressure due to each gas in the mixture is called the **partial pressure** of that gas, and is *proportional to the quantity* of the gas. Hence if the total pressure of the mixture is measured and its composition is determined by analysis the partial pressure of each gas is at once known. Take for instance, ordinary air when the barometer stands at 760 mm. (30 inches of mercury). The partial pressure of the oxygen is $\frac{21}{100} \times 760 = 159{\cdot}6$ mm. (6·3 inches of mercury), and that of the nitrogen is $\frac{79}{100} \times 760 = 600{\cdot}4$ mm. (23·7 inches of mercury).

When a gas is in contact with a liquid some of the gas is absorbed by the liquid, the amount being dependent on the pressure of the gas. If *two* gases of equal solubility are in contact with the *same* liquid they will be absorbed in quantities proportional to their respective partial pressures in the space over the liquid, and when the absorption is complete the partial pressures of the gases in the liquid are the same as the partial pressures of the gases in the space. If the partial pressure of one of the gases be made less in the space over the liquid, then some of that gas will make its exit from the liquid; and if its partial pressure be, on the other hand, increased, then more of that gas will enter the liquid. Thus we see that changes in the partial pressures of the gases in contact with the liquid determine

the exit and entry of those gases from and into the liquid. Further, since gases diffuse readily through thin porous films, the statements we have just made will, broadly speaking, hold equally good in the case when the surface of the fluid is separated from the neighbouring gases by a thin, moist, porous film.

The air in the alveoli of the lungs is a mixture of gases separated by the thin, moist, filmy wall of the capillaries from the venous blood brought to them by the pulmonary artery; and what we have now to consider is whether, in the absence of any other obvious cause, the differences of partial pressure between the gases in that air and the same gases in that blood are sufficient to account for the interchange by which the venous blood becomes arterial.

Now the oxygen and carbonic acid in blood are not in mere solution but largely in combination with certain constituents of the corpuscles and plasma. Hence the pressures they exert are much less than they would be if they were in simple solution. But on the other hand the compounds formed by these gases in the blood are very unstable and easily dissociated or broken up, so that a sufficient difference of partial pressure on the surface of the blood may still easily start the interchange between the blood and the alveolar air and between the blood and the tissues.

The partial pressures of oxygen and carbonic acid in alveolar air are usually about 100 and 40 mm. of mercury respectively. By applying these data we find that venous blood in contact with oxygen at the partial pressure it has in alveolar air becomes arterialised as regards its oxygen. And the entry of the oxygen is further assisted by the fact that it is stowed away in loose chemical combination in the red corpuscles. Similarly we may say that the exit of carbonic acid is due to the difference between the

(lower) partial pressure of carbonic acid in the alveolar air and the (higher) partial pressure it has in the venous blood; but the case is not quite so clear as it is in respect of the entry of oxygen. For the partial pressure of carbonic acid in alveolar air is not inconsiderable, and its exit from the blood is opposed by the fact that it is in loose combination with some constituent of the plasma.

The blood thus fully arterialised is whirled away to the tissues, where it becomes once more venous. In the tissues the causes of the change are much more easily understood, for the living tissues are greedy of oxygen, which they stow away in compounds so stable that they give up no oxygen to the vacuum of even the most powerful pump; the partial pressure of oxygen in the tissues may even be zero. Hence oxygen readily passes over from the arterial blood. Again, the living tissues are always producing carbonic acid in greater or less amount according as they are more or less active; the partial pressure of carbonic acid is therefore high in the tissues and quite sufficient to account for the passage of this gas from them into the neighbouring arterial blood.

The amount of oxygen left in venous blood is dependent on the varying activity of the tissues and of the quantity of blood which is flowing through them, and this is the reason why the volume of this gas was given (p. 125) as varying from eight to twelve volumes in each hundred volumes of venous blood and indeed it may even vary within wider limits.

10. The Nervous Mechanism of Respiration.—Of the various mechanical aids to the respiratory process, the nature and workings of which have now been described, one, the elasticity of the lungs, is of the nature of a dead, constant force. The action of the rest of the apparatus is under the control of the nervous system, and varies from time to time.

As the nasal passages cannot be closed by their own action, air has always free access to the pharynx; but the glottis, or entrance to the windpipe, is completely under the control of the nervous system—the smallest irritation about the mucous membrane in its neighbourhood being conveyed, by its nerves, to that part of the cerebro-spinal axis which is called the **spinal bulb** or **medulla oblongata** (see Lesson XI.). The spinal bulb thus stimulated gives rise, by a process which will be explained hereafter, termed *reflex action*, to the contraction of the muscles which close the glottis, and commonly, at the same time, to a violent contraction of the expiratory muscles, producing a cough (see p. 146). The muscular fibres of the smaller bronchial tubes are similarly under the control of the bulb, sometimes contracting so as to narrow and sometimes relaxing so as to permit the widening of the bronchial passages.

These, however, are mere incidental actions. The whole respiratory machinery is worked by a nervous apparatus. From what has been said, it is obvious that there are many analogies between the circulatory and the respiratory apparatus. Each consists, essentially, of a kind of pump which distributes a fluid (liquid in the one case, gaseous in the other) through a series of ramified distributing tubes to a system of cavities (capillaries or air-cells), the volume of the contents of which is greater than that of the tubes. While the heart however is a force-pump, the respiratory machinery represents a suction-pump.

In each the pump is the cause of the motion of the fluid, though that motion may be regulated, locally, by the contraction or relaxation, of the muscular fibres contained in the walls of the distributing tubes. But, while the rhythmic movement of the heart chiefly depends upon an apparatus placed within itself, which is then controlled by the central nervous system, that of the respiratory apparatus results mainly from the operation of a

nervous centre lodged in the spinal bulb, which has been called the **respiratory centre.**

This centre is situated (see Fig. 49, *R.C.*) close to the two previously described (Figs. 22 and 23) as the vaso-motor and cardio-inhibitory centres (pp. 69 and 75). Impulses arise in this centre, pass down the spinal cord, and leaving the cord along certain nerves, reach the various muscles by whose contractions the movements of respiration are produced. The respiratory muscles contract only when they receive these impulses, and therefore all the movements of respiration depend upon the activity of this centre, and cease at once on injury of this part of the spinal bulb.

The action of the centre is primarily *automatic;* in other words the impulses it sends out appear to be the result of changes *started within itself,* in the same way that the beat of the heart is automatic as the outcome of changes started in the muscle-tissue of which it is made up. This primary automatism of the respiratory centre is subject, however, to control by impulses reaching it from outlying parts of the body, and more particularly by changes in the condition or quality of the blood which circulates in the capillaries of the centre itself, in a way to be described presently.

The intercostal muscles are supplied by **intercostal nerves** coming from the spinal cord in the region of the back (Fig. 49, *ICN*, *ICN*, *ICN*), and the muscular fibres of the diaphragm are supplied by two nerves, one on each side, called the **phrenic nerves** (Fig. 49, *Phr.*), which starting from certain of the spinal nerves in the neck, dip into the thorax at the root of the neck, and find their way through the thorax by the side of the lungs to the diaphragm, over which they are distributed. Now from the nervous respiratory centre in the spinal bulb impulses at repeated intervals descend along the upper part of the spinal cord and, passing out by the phrenic and intercostal nerves

respectively, reach the diaphragm and the intercostal muscles. These immediately contract, and thus an inspiration takes place. Thereupon the impulses cease, and are replaced by other impulses, which though starting from the same centre pass, not to the diaphragm and external intercostal muscles, but to other, expiratory, muscles, which they throw into contraction, and thus expiration is brought out. As a general rule the inspiratory impulses are much stronger than the expiratory; indeed, in ordinary quiet breathing expiration is chiefly brought about, as we have seen, by the elastic recoil of the lungs and chest walls; these need no nervous impulses to set them at work, as soon as the inspiratory impulses cease and the diaphragm and other inspiratory muscles leave off contracting, they come of themselves into action. But, in laboured breathing, very powerful expiratory impulses may leave the respiratory centre and pass to the various muscles whose contractions help to drive the air out of the chest.

Every day experience shows that no function of the body is more obviously subject to sudden and marked changes than is the respiration. It is quickened by exercise, quickened or slowed by emotions; hurried by stimulation of the skin, as by a dash of cold water, or brought to a standstill by stimulating the mucous membrane of the nose by a pungent vapour such as strong ammonia. The changes involved in sneezing, laughing, coughing, &c., are profound and peculiar. Finally we can control our respiration by an effort of the will within very wide limits and in almost any desired way. The mechanism involved in the production of all these changes is correspondingly complicated; but certain broad facts are fairly simple, and to these we may now turn.

The main trunk of the **vagus** nerve (see Lesson XI.) gives off a branch to the larynx as it passes down the neck (Fig. 49, *S.Lr.*). If the vagus be cut *below the point of exit* of this nerve (as at *x*, Fig. 49) and the upper (central)

end (y, Fig. 49), connected with the spinal bulb be stimulated, the respiration becomes hurried. Thus we have in

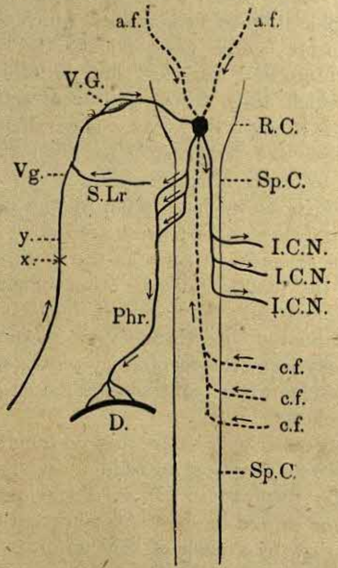

FIG. 49.—DIAGRAM TO ILLUSTRATE THE POSITION OF THE RESPIRATORY CENTRE, THE CONNECTIONS OF THIS CENTRE WITH THE INTERCOSTAL MUSCLES AND DIAPHRAGM, AND THE PATHS BY WHICH IMPULSES PASS TO THE CENTRE FROM OUTLYING PARTS OF THE BODY AND FROM THE BRAIN.

Sp.C, *Sp.C*, spinal cord; *R.C*, respiratory centre in the bulb; *ICN*, *ICN*, *ICN*, three intercostal nerves; *Phr.* one phrenic nerve passing to the diaphragm *D*; *Vg.* vagus nerve; *V.G*, ganglion of vagus nerve; *S.Lr*, superior laryngeal nerve. The dotted lines, *cf*, *cf*, *cf*, indicate paths of conduction for impulses to the respiratory centre from some part of the body such as the skin; the dotted lines, *af*, *af*, similar paths from the brain to the centre. The arrows show the direction in which impulses travel along each nerve or path.

the *vagus* a nerve such that impulses passing up it may *quicken* the respiration by their action on the respiratory centre.

If on the other hand the branch of the vagus supplying the larynx, the **superior laryngeal nerve**, be cut, and its central end be stimulated, the result is that the respiration may be *slowed*, even to a *complete cessation* of all respiratory movements.

In the case of the vagus impulses seem to be ordinarily always passing up it to facilitate the action of the respiratory centre, for if the vagus nerves be simply cut, the respiration becomes at once extremely slow.

These two nerves may be taken as typical of their kind, the one quickening, the other slowing the respiration. But similar nerves run to the respiratory centre from all parts of the body, notably from the skin, also from the brain, and by their varied action largely determine the manifold changes which the respiratory movements from time to time undergo.

11. Influence of Blood-Supply on the Respiratory Centre. Dyspnœa and Asphyxia.—The function of respiration has for its one great object the conversion of venous into arterial blood. Hence we might expect that the mechanism which controls it should be adjusted so as to be extremely sensitive to the varying condition or quality of the fluid (blood), whose gaseous composition it has to regulate. This expectation is justified by facts, for although the respiratory centre is keenly responsive to impulses brought to bear upon it along various nerves, it is even more so to the influence exerted by the varying quality of the blood circulating in the capillaries of the spinal bulb. Thus, when by any means the blood becomes less arterialised than it should be, the respiratory centre feels this change, and is at once stimulated to greater activity in the endeavour, by an increased force and frequency of the respiratory movements, to restore the blood to its proper condition. In other words, venous blood makes the respiratory centre work faster and more vigorously.

The blood becomes more venous whenever the free

access of air to the lungs is interfered with; as, for instance, when a man is strangled, drowned, or choked by food or other obstacle in the trachea. But the blood may become unusually venous by means less violent than the above. Since the rapidity of diffusion between two gaseous mixtures depends on the difference of the proportions in which their constituents are mixed, it follows that the more nearly the composition of the tidal air approaches that of the stationary air, the slower will be the diffusion of oxygen inwards, and of carbonic acid outwards, and the more deficient in oxygen and overcharged with carbonic acid will the air in the alveoli become. Thus by breathing in a confined space, the oxygen in the tidal air is *gradually* diminished and the carbonic acid *gradually* increased until at length a point is reached when the change effected in the stationary air is too slight to enable it to supply the pulmonary blood with oxygen, and to relieve it of carbonic acid to the extent required for its proper arterialisation.

When from any of the above causes the blood sent to the respiratory centre is more venous than usual, the centre is stimulated and the respiratory movements become quicker and more forcible. This condition is usually spoken of as **dyspnœa**, or laboured breathing. It is characterised by the increased force and frequency with which both the inspiratory and expiratory muscles contract. If the offending cause of dyspnœa be not removed, the blood becomes more and more venous. By this means the respiratory centre is spurred on to still greater activity. Not only do the ordinary muscles of respiration contract more vigorously, but the accessory muscles (p. 145) come into more prominent play, and *chiefly those which assist expiration*. Still later, nearly all the muscles of the body are thrown into a state of violent contracting activity, and with the onset of these **convulsions** dyspnœa passes over into **asphyxia**. The violence of the convulsive movements speedily leads to exhaustion, and the con-

vulsions cease. After this stage is reached, a long-drawn inspiration takes place at intervals; but the intervals become longer and longer and the inspiratory movements more and more feeble until the last breath is taken and breathing ends with an expiratory gasp.[1]

After death by asphyxia the blood throughout the whole body is of course venous. The right side of the heart, the great (systemic) veins and the pulmonary arteries are highly distended with blood, while the left side of the heart is empty. This condition of the vascular system is brought about largely by an obstruction to the usually easy flow of blood through the lungs, which is due to a constriction of their small arteries caused by the stimulation resulting from the venosity of the blood. But it is helped by the unusually forcible drawing of blood into the great veins which results from the increased force of the respiratory movements (see p. 166).

Venous blood is distinguished from arterial by two features, by having less oxygen and more carbonic acid. Hence, in asphyxia, two influences of a distinct nature are co-operating; one is the *deprivation of oxygen*, the other is the *excessive accumulation of carbonic acid* in the blood. Oxygen starvation and carbonic acid poisoning, each of which is injurious in itself, are at work together.

The respiratory centre is very sensitive to variations in the normal quantity of carbonic acid in the blood. We have already stated that the carbonic acid in the alveolar air exerts a partial pressure of 40 mm. of mercury, this corresponds very closely to the pressure of carbonic acid in the blood leaving the lung and reaching the respiratory centre. If this pressure of carbonic acid be raised by even a few millimetres the respiration

[1] The term asphyxia is sometimes used to include all the above three stages, from the onset of dyspnœa until death ensues.

becomes accelerated. Indeed, if the amount of acid, of whatever kind it may be, in the arterial blood be materially increased, the respiratory centre is stimulated and respiration is quickened. Small changes in the partial pressure of oxygen in the air breathed do not affect the respiratory rhythm but great deprivation of oxygen rapidly produces the symptoms of asphyxia. The reason of this is that in the absence of a sufficient supply of oxygen the combustion in the tissues is incomplete, large quantities of acid substances are formed as the result, these are thrust into the blood where they accumulate, and stimulate the respiratory centre to make the desperate efforts which are characteristic of asphyxia. The acids produced in the tissues, in their stimulating action on the respiratory centre, act as hormones (p. 27).

That the lack of oxygen is an important thing is further shown by the asphyxiating effects of certain poisonous gases. Thus sulphuretted hydrogen, so well known by its offensive smell, has long had the repute of being a positive poison. But its evil effects appear to arise chiefly, if not wholly, from the circumstance that its hydrogen combines with the oxygen carried by the blood-corpuscles, and thus gives rise, indirectly, to a form of oxygen starvation.

Carbonic oxide gas (carbon monoxide, CO) has a much more serious effect, as it turns out the oxygen from the blood-corpuscles, and forms a very stable combination of its own with the hæmoglobin. The compound thus formed is only very gradually decomposed by fresh oxygen, so that if any large proportion of the blood-corpuscles be thus rendered useless, the animal dies before restoration can be effected. Badly made common coal gas sometimes contains 20 to 30 per cent. of carbon monoxide; and, under these circumstances, a leakage

of the pipes in a house may be extremely perilous to life.

12. The Influence of Respiration on the Circulation. —Just as there are certain secondary phenomena which accompany, and are explained by, the action of the heart, so there are secondary phenomena which are similarly related to the working of the respiratory apparatus. Of these the chief is the effect of the inspiratory and expiratory movements upon the circulation.

In consequence of the elasticity of the lungs, a certain force must be expended in distending them, and this force is found experimentally to become greater and greater the more the lung is distended; just as, in stretching a piece of india-rubber, more force is required to stretch it a good deal than is needed to stretch it only a little. Hence, when inspiration takes place, and the lungs are distended with air, the heart and the great vessels in the chest are subjected to a less pressure than are the blood-vessels of the rest of the body.

For the pressure of the air contained in the lungs is exactly the same as that exerted by the atmosphere upon the surface of the body; that is to say, fifteen pounds on the square inch. But a certain amount of this pressure exerted by the air in the lungs is counterbalanced by the elasticity of the distended lungs. Say that in a given condition of inspiration a pound [1] pressure on the square inch is needed to overcome this elasticity, then there will be only fourteen pounds pressure on every square inch of the heart and great vessels. And hence the pressure on the blood in these vessels will be one pound per square inch less than that on the veins and arteries of the rest of the body, which lie outside the thorax. If there were no aortic, or pulmonary, valves, and if the structure of the

[1] A "pound" is stated here for simplicity's sake. As a matter of fact the pressure required is much less than this, not more than 2 or 3 ounces.

vessels, and the pressure upon the blood in them, were everywhere the same, the result of this excess of pressure on the surface would be to drive all the blood from the arteries and veins of the rest of the body into the heart and great vessels contained in the thorax. And thus the diminution of the pressure upon the thoracic blood cavities produced by inspiration, would, practically, suck the blood from all parts of the body towards the thorax. But the suction thus exerted, while it hastened the flow of blood to the heart in the veins, would equally oppose the flow from the heart to the arteries, and the two effects might balance one another.

As a matter of fact, however, we know—

(1) That the blood in the great arteries is constantly under a very considerable pressure, exerted by their elastic walls; while that of the veins is under little pressure.

(2) That the walls of the arteries are strong and resisting, while those of the veins are weak and flabby.

(3) That the veins have valves opening towards the heart; and that, during the diastole, there is no resistance of any moment to the free passage of blood into the heart; while, on the other hand, the cavity of the arteries is shut off from that of the ventricle, during the diastole, by the closure of the semilunar valves.

Hence it follows that equal pressures applied to the surface of the veins and to that of the arteries must produce very different effects. In the veins the pressure is something which did not exist before; and partly from the presence of valves, partly from the absence of resistance in the heart, partly from the presence of resistance in the capillaries, it all tends to accelerate the flow of blood *towards* the heart. In the arteries, on the other hand, the pressure is only a fractional addition to that which existed before; so that, during the systole, it only makes a comparatively small addition to the resistance which has to

be overcome by the ventricle ; and during the diastole, it superadds itself to the elasticity of the arterial walls in driving the blood onwards towards the capillaries, inasmuch as all progress in the opposite direction is stopped by the semilunar valves.

It is, therefore, clear, that the inspiratory movement, on the whole, helps the heart, inasmuch as its general result is to drive the blood the way that the heart propels it.

In expiration, the difference between the pressure of the atmosphere on the surface, and that which it exerts on the contents of the thorax through the lungs, becomes less and less in proportion to the completeness of the expiration. Whenever, by the ascent of the diaphragm and the descent of the ribs, the cavity of the thorax is so far diminished that pressure is exerted on the great vessels, the veins, owing to the thinness of their walls, are especially affected, and a check is given to the flow of blood in them, which may become visible as a *venous pulse* in the great vessels of the neck. In its effect on the arterial trunks, expiration, like inspiration, is, on the whole, favourable to the circulation ; the increased resistance to the opening of the valves during the ventricular systole being more than balanced by the advantage gained in the addition of the expiratory pressure to the elastic reaction of the arterial walls during the diastole.

When the skull of a living animal is laid open and the brain exposed, the cerebral substance is seen to rise and fall synchronously with the respiratory movements ; the rise corresponding with expiration, and being caused by the obstruction thereby offered to the flow of the blood in the veins of the head and neck.

The effects of the respiratory movements on the flow of blood towards the heart must be the same for any other structure contained in the thorax and connected with vessels lying outside the thorax. Now the thoracic duct

is a large, thin-walled tube placed inside the thorax and communicating with the lymphatic vessels which lie in the abdomen, and, further, it is plentifully supplied with valves. At inspiration the reduction of pressure on the outside of the duct draws lymph up into it from the abdominal lymphatic vessels. At expiration, the lymph cannot pass down again, owing to the valves in the duct, and is therefore sent on towards the junction of the duct with the venous system. Hence the respiratory movements on the whole are a not unimportant aid to the onward flow of lymph (see p. 92).

13. **Ventilation.**—In the case of breathing the same air over and over again the deprivation of oxygen, and the accumulation of carbonic acid, cause injury, long before any signs of even dyspnœa are observed. Under these circumstances uneasiness and headache arise when less than 1 per cent. of the oxygen of the air is replaced by other matters; the symptoms in this case however are due not so much to the diminution of oxygen or the increase of carbonic acid, as to the poisonous effects of the various organic matters present in expired air which, though existing in minute quantities, have a powerfully deleterious action. It need hardly be added that the persistent breathing of such air tends to lower all kinds of vital energy, and predisposes to disease. Hence the necessity of sufficient air and of ventilation for every human being.

The object of ventilation is to prevent the accumulation of these organic impurities (p. 151). Since the organic matter does not admit of direct estimation, the percentage of carbonic acid in the air is usually taken as an indirect measure of its amount. Air which has been fouled by breathing is injurious if it contains more than ·05 per cent. of carbonic acid. Knowing the amount of air passed through the lungs in one hour and the amount of carbonic acid it contains (p. 152), calculation easily shows

that if the percentage of carbonic acid is to be kept down to the limit of ·05 per cent. a man should live in a room whose capacity is not less than 28,000 litres (1,000 cubic feet) and into which at least 60,000 litres (2,000 cubic feet) of fresh air are admitted each hour.[1]

[1] A cubical room nine feet high, wide and long, contains only 729 cubic feet of air.

LESSON V

THE SOURCES OF LOSS AND OF GAIN TO THE BLOOD

1. General Review of the Gain and Loss.—The blood which has been aërated, or arterialised, by the process described in the preceding Lesson, is carried from the lungs by the pulmonary veins to the left auricle, and is then forced by the auricle into the ventricle, and by the ventricle into the aorta. As that great vessel traverses the thorax, it gives off several large arteries, by means of which blood is distributed to the head, the arms, and the walls of the body. Passing through the diaphragm (Fig. 47, *Ao.*), the aortic trunk enters the cavity of the abdomen, and becomes what is called the *abdominal aorta*, from which vessels are given off to the viscera of the abdomen. Finally, the main stream of blood flows into the *iliac* arteries, whence the viscera of the pelvis and the legs are supplied.

Having in the various parts of the body traversed the ultimate ramifications of the arteries, the blood, as we have seen, enters the capillaries. Here the products of the waste of the tissues constantly pour into it ; and, as the blood is everywhere full of corpuscles, which, like all other living things, decay and die, the products of their decomposition also tend to accumulate in it, but these are insignificant compared to those coming from the great mass of the tissues. It follows that, if the blood is to be kept pure, the waste matters thus incessantly poured into,

or generated in it, must be as constantly got rid of, or excreted.

Three distinct sets of organs are especially charged with this office of continually removing or "excreting" waste matters from the blood. They are the *lungs*, the *kidneys*, and the *skin* (see Lesson I.). These three great organs may therefore be regarded as so many drains from the blood—as so many channels by which it is constantly losing substance.

On the other hand, the blood, as it passes through the capillaries, is constantly giving up material by exudation through the capillary walls into the surrounding tissues, in order to supply them with nourishment, and thus in this way also is constantly losing matter.

The material which the blood loses by giving it up to the tissues consists of complex organic bodies, such as proteids, fats, carbohydrates, and various substances manufactured out of these, of certain salts, of a large quantity of water, and lastly of oxygen.

The material which the blood loses by giving it up to the skin, lungs and kidneys, passes away from these organs as water, as carbonic acid, as peculiar organic substances of which one, called *urea*, is much more abundant than the others, and as certain inorganic salts. Speaking generally we may say that these organs together excrete from the blood, water, carbonic acid, urea and salts.

Another kind of loss takes place from the surface of the body generally, and from the interior of the air-passages. Heat is constantly being given off from the former by radiation, evaporation, and conduction : from the latter, chiefly by evaporation ; and the loss of heat in each case is borne by the blood passing through the skin and air-passages respectively. Besides this a certain quantity of heat is lost by the urine and fæces which are always warm when they leave the body.

On the side of gain we have, in the first place, the

various substances which are the products of the activity of the several tissues, muscles, brain, glands, &c., and which pass from the tissues into the blood. We may speak of these as waste products, and one of them which is produced by all the tissues, namely carbonic acid, is emphatically a waste product and is got rid of as soon as possible. But some of the substances which are returned to the blood from the tissues are not wholly useless matters to be thrown off as rapidly as possible; they are capable of being used up again by some tissue or other. Thus, as we shall see, the liver, at certain times at all events, returns to the blood a certain quantity of sugar which is made use of in other parts of the body, and similarly the spleen, while it takes up certain substances from the blood, gives back to the blood certain other substances which we can hardly speak of as waste matters in the sense of being useless material fit only to be at once thrown away.

In the second place, the blood is continually receiving from the alimentary canal the materials arising from the food which has been digested there. As we shall see, some of this material passes directly from the cavity of the alimentary canal into the blood, but some of it goes in a more roundabout way through what are called the lacteals or lymphatics. On its way to the blood this latter is joined by material which, escaping from the blood and not used by the tissues, or passing from the tissues directly into the lymphatics, is carried back to the blood by the thoracic duct (see Lesson II., p. 87).

In the third place, the blood is continually gaining oxygen from the air through the lungs.

Then again the blood, while it loses heat by the skin and lungs, gains heat from the tissues. As we have already seen (Lesson I., p. 25) oxidation is continually going on in various parts of the body, and by this oxidation heat is continually being set free. Some of this oxidation may take place in the blood itself; we do not know exactly how

much, but probably very little. The greater part of the heat is generated in the tissues, in the muscles and elsewhere, and is given up by the tissues to the blood. So that we may say that the blood gains heat from the tissues.

These several gains and losses are for the most part going on constantly, but are greater at one time than at another. Thus the gain to the blood from the alimentary canal is much greater some time after a meal than just before the next meal, though unless the meals be very far apart indeed, the whole of the material of one meal has not passed into the blood before the next meal is begun. Again, though the muscles, even when completely at rest, are taking up oxygen and nutritive material, and giving out carbonic acid and other waste products, they give out and take in much more when they are at work. So also certain "secreting glands" as they are called, which we shall study presently, such as the salivary glands, have periods of repose; it is at certain times only, as when food has been taken, that they pour out any appreciable quantity of fluid. Hence though they are probably taking up material from the blood and storing it up in their substance even when they appear at rest, they take up much more and so become much more distinctly means of loss to the blood, when they are actively pouring out their secretions.[1] In the case of the liver the loss to the blood is more constant, since the secretion of bile as we shall see is continually going on, though greater at certain times than at others; and the materials for the bile have to be provided by the blood. Some of the constituents of the bile, however, pass back from the

[1] The word "secretion" is used by physiologists in two senses. Primarily it is used to denote the sum total of the processes by which a gland or organ *forms* the fluid which it gives out; thus we say that the salivary glands "secrete" saliva. But the fluid thus formed is itself spoken of as "a secretion." The word "excretion" is usually applied to any fluid which after its formation is useless and requires to be at once got rid of. Thus we say that urine is an excretion which is secreted (*i.e.* formed) by the kidneys; and we speak of those secretory structures which get rid of waste as excretory organs.

intestines into the blood; and so far the loss to the blood by the liver is temporary only.

Of all the gains to the blood perhaps the most constant is that of oxygen, and of all the losses perhaps the most constant is that of carbonic acid; but even these vary a good deal at different times or under different circumstances.

Broadly speaking then the blood gains oxygen from the lungs, complex organic food materials from the alimentary canal, and various substances which we may speak of as waste substances from the several tissues; and it loses on the one hand material which we may speak of as constructive material to the several tissues; and on the other hand material which passes away by the skin, lungs, and kidney, as water, carbonic acid, urea, and saline bodies. And while it is continually receiving heat from the several tissues, it is also continually losing heat by the skin, lungs, and other free surfaces of the body.

The sources of loss and gain to the blood may be conveniently arranged in the following tabular form:—

SOURCES OF LOSS AND GAIN TO THE BLOOD.[1]

A. SOURCES OF LOSS:—

I. *Loss of Matter.*

1. The lungs: carbonic acid and water (fairly constant).
2. The kidneys: urea, water, salines (fairly constant).
3. The skin: water, salines (fairly constant).
4. The tissues: constructive material (variable especially in the case of those tissues whose activity is intermittent, such as the muscles, many secreting glands, &c.), water, &c., to form lymph.

[1] The learner must be careful not to confound the losses and gains of the *blood* with the losses and gains of the *body* as a whole. The two differ in much the same way as the internal commerce of a country differs from its export and import trade.

II. *Loss of Heat.*

1. The skin.
2. The lungs.
3. The excretions by the kidney and the alimentary canal.

B. Sources of Gain :—

I. *Gain of Matter.*

1. The lungs : oxygen (fairly constant).
2. The alimentary canal : food (variable).
3. The tissues : products of their activity, waste matters (always going on but varying according to the activity of the several tissues).
4. The lymphatics : lymph (always going on but varying according to the activity of the several tissues).[1]

II. *Gain of Heat.*

1. The tissues generally, especially the more active ones, such as the muscles.
2. The blood itself, probably to a very small extent.

2. The Kidneys.—In the preceding Lesson we have described the operation by which the lungs withdraw from the blood much carbonic acid and water, and supply oxygen to the blood: we now proceed to the second source of continual loss, the Kidneys.

Of these organs, there are two, placed at the back of the abdominal cavity, one on each side of the lumbar region of the spine. Each, though somewhat larger than the kidney of a sheep, has a similar shape. The depressed, or concave, side of the kidney is turned inwards, or towards the spine ; and its convex side is directed outwards (Fig. 50). From the middle of the concave side (called the

[1] The gain from those lymphatics which are called lacteals, since it comes from the alimentary canal, varies much more.

hilus) of each kidney, a long tube with a small bore, the **Ureter** (*Ur.*), proceeds to the **Bladder** (*Bl.*).

The latter, situated in the pelvis, is an oval bag, the walls of which contain abundant unstriped muscular fibre, while it is lined, internally, by mucous membrane, and coated externally by a layer of the *peritoneum*, or double

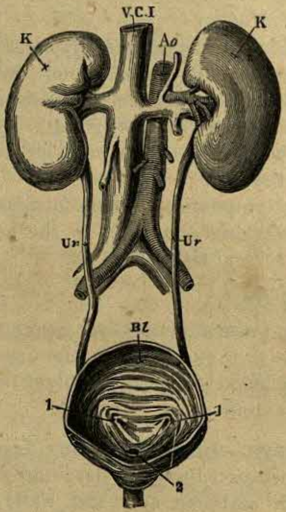

FIG. 50.

The kidneys (*K*); ureters (*Ur.*); with the aorta (*Ao.*); and vena cava inferior (*V.C.I.*); and the renal arteries and veins. *Bl.* is the bladder, the top of which is cut off so as to show the openings of the ureters (1, 1) and that of the urethra (2).

bag of serous membrane which has exactly the same relations to the cavity of the abdomen and the viscera contained in them as the pleuræ have to the thoracic cavity and the lungs. The ureters open side by side, but at some little distance from one another, on the posterior and inferior wall of the bladder (Fig. 50, 1, 1). Each

ureter is lined by an epithelium consisting of several layers of cells. Outside of these is a muscular coat made up of unstriated muscle-fibres, arranged in two layers and surrounded externally by some fibrous connective tissue. In front of the ureters is a single aperture which leads into the canal called the **Urethra** (Fig. 50, 2), by which the cavity of the bladder is placed in communication with the exterior of the body. The openings of the ureters enter the walls of the bladder obliquely, so that it is much more easy for the fluid to pass from the ureters into the bladder than for it to get the other way, from the bladder into the ureters.

Mechanically speaking, there is little obstacle to the free flow of fluid from the ureters into the bladder, and from the bladder into the urethra, and so outwards; but certain muscular fibres arranged circularly around the part called the "neck" of the bladder, where it joins the urethra, constitute what is termed a **sphincter**, and are usually, during life, in a state of contraction, so as to close the exit of the bladder, while the other muscular fibres of the organ are relaxed.

It is only at intervals that this state of matters is reversed; and the walls of the bladder contracting, while its sphincter relaxes, its contents, the **urine**, are discharged. But, though the expulsion of the secretion of the kidneys from the body is thus intermittent, the excretion itself is constant. The urinary fluid is propelled drop by drop along the ureters by rhythmic contractions which pass along their walls in the direction of the bladder where it accumulates, until its quantity is sufficient to give rise to the uneasy sensations which compel its expulsion.

3. **The Structure of a Kidney.**—When a longitudinal section of a kidney is made (Fig. 51), the upper end of the ureter (*U*) seems to widen out into a basin-like cavity (*P*), which is called the **pelvis** of the kidney. Into this sundry conical elevations, called the **pyramids** (*Py*)

project; and their summits present multitudes of minute openings—the final terminations of the **tubules**, of which the thickness of the kidney is chiefly made up. If the tubules be traced from their openings towards the outer surface, they are found, at first, to lie parallel with one another in bundles, which radiate towards the surface, and subdivide as they go; but at length they spread about irregularly, and become coiled and interlaced. From this

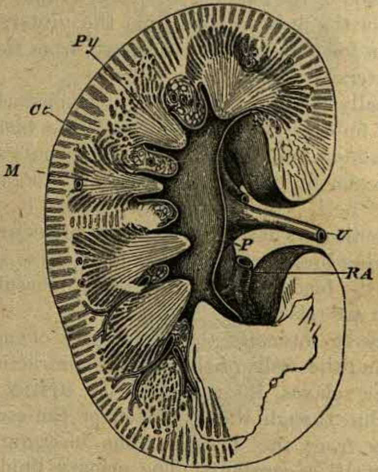

FIG. 51.—LONGITUDINAL SECTION OF THE HUMAN KIDNEY.

Ct, the cortical substance; *M*, the medullary substance; *P*, the pelvis of the kidney; *U*, the ureter; *R.A*, the renal artery; *Py*, the pyramids.

circumstance, the middle part, or **medulla** (*medulla*, marrow) of the kidney looks different from the superficial part or **cortex** (*cortex*, bark); but, in addition, the cortical part is more abundantly supplied with vessels than the medullary, and hence has a darker aspect. Each tubule after a very devious course ultimately terminates in a dilatation (Fig. 52) called a **Malpighian capsule.**

Into the summit of each capsule, a small vessel (Figs. 52 and 53, *v.a*), one of the ultimate branches of the **renal artery**, which reaches the kidney at the concave side, with the ureters, and divides into branches which pass in between the pyramids (Fig. 51, *RA*), enters (driving the thin wall of the capsule before it), and immediately breaks up into a bunch of looped capillaries, called a **glomerulus** (Fig. 52 *gl*), which nearly fills the cavity of the capsule. The blood is carried away from this glomerulus

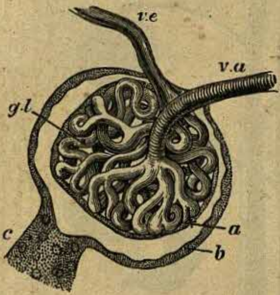

FIG. 52.—A MALPIGHIAN CAPSULE (HIGHLY MAGNIFIED).

v.a, small branch of renal artery entering the capsule, breaking up into the glomerulus, *g.l*, and finally joining again to form the vein, *v.e.*
c, the tubule; *a*, the epithelium over the glomerulus; *b*, the epithelium lining the capsule.

by a small vein or vessel (*ve*), which does not, at once, join with other veins into a larger venous trunk, but opens into the network of capillaries (Fig. 53) which surrounds the tubule, thus repeating the portal circulation on a small scale.

The course of the tubules is devious and peculiar. After leaving the capsule each tubule becomes twisted and is spoken of as **convoluted** (Fig. 54, II.). Passing towards the medulla, at first in a slightly **spiral** course, it proceeds straight down into the pyramid, where it bends

back upon itself and runs up again into the cortex. The loop thus formed is known as the **loop of Henle,**[1] and the two parts of which it is formed are called the **descending limb** and the **ascending limb** of the loop (Fig. 54, III. IV.).

Reaching the cortex once more the tubule becomes **zigzag** and then again **convoluted.** after which it

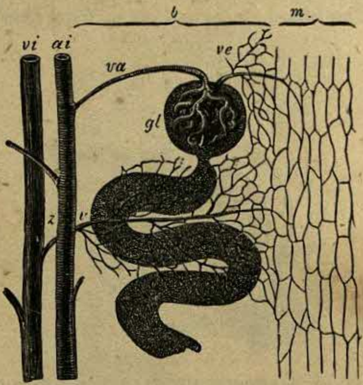

FIG. 53.—CIRCULATION IN THE KIDNEY.

ai, small branch of renal artery giving off the branch *va*, which enters glomerulus, issues as *ve*, and then breaks up into capillaries, which after surrounding the tubule find their way by *v* into *vi*, branch of the renal vein; *m*, capillaries around tubules in parts of the cortical substance where there are no glomeruli.

passes into a straight part or **collecting tubule,** which, leaving the cortex finally for the medulla and uniting with other similar collecting tubules, forms the discharging tubule which finally opens near the summit of a pyramid (Fig. 54, V.-IX.).

Each tubule is lined throughout by cells, the epithelium, and the cells differ in their characters in the several

[1] Who first described it.

parts of its course. The details of these differences are numerous and complicated, but the following statement includes all that is most essential. The cells in the convoluted, spiral and zigzag portions are, on the whole, large, very granular and striated, and both the

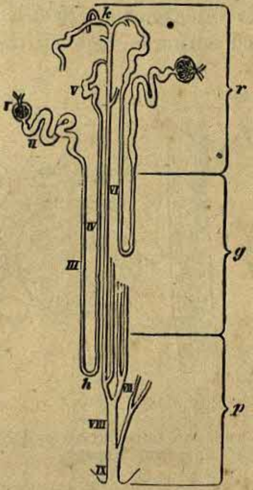

FIG. 54.—DIAGRAMMATIC VIEW OF THE COURSE OF THE TUBULES IN THE KIDNEY.

r, cortical portion answering to *Ct* in Fig. 51, *k* being close to the surface of the kidneys; *g*, *p*, medullary portion, *p* reaching to the summit of the pyramid.

IX, opening of tubule on the pyramid; *VIII*, *VII*, *VI*, the straight portion of the tubules; *V–II*, the twisted portion of the tubules; *I*, the Malpighian capsule.

cells and their nuclei stain readily and deeply. In the collecting tubules the cells are flattened, cubical, quite free from granules and do not stain readily. In the loop of Henle the cells of the descending limb resemble those in the collecting tubules in being flattened and

free from granules; the cells of the ascending limb, though small, are somewhat granular and often striated and thus present affinities to the cells of the convoluted tubules. These two chief types of cells are shown in Fig. 55.

The artery which supplies the kidney enters at the hilus and divides into branches which pass round the pelvis and proceed outwards between the pyramids. At

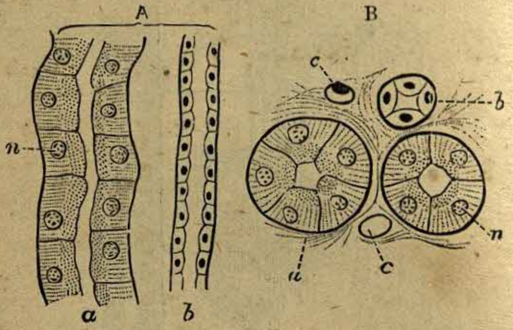

FIG. 55.—TYPES OF THE TWO CHIEF KINDS OF CELLS IN THE TUBULES OF THE KIDNEY.

A, tubules cut lengthwise; B, tubules cut across.
a, type of (secreting) cell lining the convoluted (spiral and zigzag) tubules; *b*, type of cells lining the conducting, collecting and discharging tubules; *n*, nuclei; *c*, in B, capillaries seen in section.

the junction of the medulla and cortex these branches spread out sideways and form arches. From these arches branches run (i) straight out to the surface of the kidney giving off smaller lateral branches, of which some pass to the capsules while others supply the capillary network round the tubules: (ii) down towards the pyramids, in whose substance they break up into capillaries. The veins also form arches at the junction of the cortex and medulla, into which the blood flows from the capillaries,

and leave the kidney by a course parallel to that of the entering arteries.

4. The Composition of Urine and Chemistry of Urea.—The renal secretion is a clear yellowish fluid,

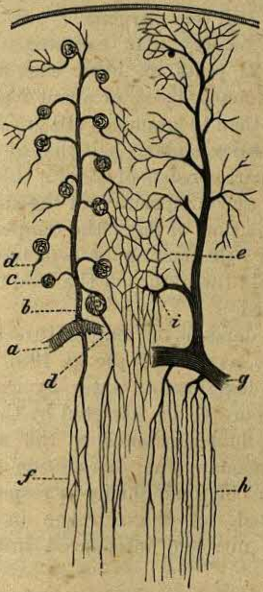

FIG. 56.—BLOOD VESSELS OF KIDNEY. (CADIAT.)

a, part of arterial arch; *b*, interlobular artery; *c*, glomerulus; *d*, efferent vessel; *e*, capillaries of cortex; *f*, small arteries of medulla; *g*, venous arch; *h*, straight veins of medulla; *i*, interlobular vein.

whose specific gravity is not very different from that of blood-serum, being 1·020. In health it has a slightly acid reaction, due to the presence of acid sodium phosphate. It is composed chiefly of water, holding in solution (i) *organic substances*, of which the chief is **urea**,

with a very much smaller amount of **uric acid**. (ii) *Inorganic salts*, chiefly sodium chloride and sulphates and phosphates of sodium, potassium, calcium and magnesium. (iii) *Colouring matters*, of which but little is known. (iv) *Gases*, chiefly carbonic acid with a very small amount of nitrogen and still less oxygen.

An average healthy man excretes about 1,500 c.c. (50 ounces or 2½ pints) of urine each day. In this are dissolved 33 grammes (1¼ oz. or about 2 per cent.) of urea and not more than ·5 grammes (10 grains) of uric acid. The amount of salts is about half that of the urea, and of this the larger part consists of sodium chloride.

The quantity and composition of the urine vary greatly according to the time of day; the temperature and moisture of the air; the fasting or replete condition of the alimentary canal; the nature of the food; and the amount of fluid consumed.

The *quantity* depends on temperature and moisture of the air, because, as we shall see (p. 198), these determine the greater or less loss of water by the skin, and thus leave less or more to be excreted by the kidneys. The relationship of fluid consumed to the amount of urine excreted is obvious. The *composition* varies with the kind and amount of food, chiefly in respect of the amount of urea excreted, for the nitrogen in urea represents nearly all the nitrogen introduced into the body as proteids.

This relationship of the nitrogen in food to the nitrogen of urea confers upon urea its supreme importance as a constituent of urine. For the body cannot make good its nitrogenous waste from any source other than the nitrogen introduced into it in the form of proteids, and the nitrogen in this waste leaves the body again chiefly as urea, a very small part reappearing in the form of uric acid. Hence variations in the quantity of urea excreted thus become the measure of the amount of nitrogen turned over or "metabolised" in the body from time to time.

Urea is a white crystalline solid, very soluble in water, and composed of carbon, oxygen, hydrogen and nitrogen. Its chemical formula is $(NH_2)_2CO$, from which it is seen to contain rather more than 46 per cent. of nitrogen. It forms characteristic crystalline compounds with nitric acid and oxalic acid, which serve for its qualitative identification. When acted on by sodium hypobromite, urea is decomposed in such a way that all the carbon becomes carbon dioxide (carbonic acid gas) and the nitrogen is given off as a gas:

$$(NH_2)_2CO + 3NaBrO = N_2 + CO_2 + 2H_2O + 3NaBr.$$

This is an important reaction, since by measuring the nitrogen evolved the urea may be estimated quantitatively; a method now very generally employed. When in solution, under the influence of a ferment sometimes secreted by the mucous membrane of the bladder, or of organisms from the air, urea takes up water and becomes ammonium carbonate;

$$(NH_2)_2CO + 2H_2O = (NH_4)_2CO_3.$$

This accounts for the ammoniacal odour of stale urine.

Historically urea is interesting as being the first organic animal product prepared (synthetically) from inorganic sources.

5. **The Secretion of Urine.**—Many of the constituents of urine are present in blood. These appear in the urine dissolved in a large quantity of water, whereas many other substances also present in the blood do not, in a state of health, make their way into the urine. This suggests the idea that the kidney is a peculiar and delicate kind of filter which allows certain substances together with a large quantity of water to pass through it, but refuses to allow other substances to pass through. And when we come to study the minute structure of the kidney we find much to support this idea. Thus we saw that the surface of the glomerulus is, practically, free, or in direct

communication with the exterior by means of the cavity of the tubule; and, further, that in each vessel of the glomerulus a thin stream of blood constantly flows, only separated from the cavity of the tubule by the capillary wall and the very delicate membrane covering the glomerulus. The Malpighian capsule may, in fact, be regarded as a funnel, and the membranous walls of the glomerulus as a piece of very delicate but *peculiar* filtering-paper, into which the blood is poured.

And indeed we have reason to think that a great deal of the water of urine together with certain of the constituents (the inorganic salts) is thus as it were filtered off by the Malpighian capsules. But it must be remembered that the process is after all very different from actual filtering through paper; for filter paper will let everything pass through that is really dissolved as well as bodies so small as blood-corpuscles, whereas the glomerulus, while letting some things through, refuses to admit others, *e.g.* the proteins of the plasma, even though they are in a state of solution.

Speaking of the process, with this caution, as one of filtration, it is obvious that the more full the glomerulus is of blood the more rapid will be the escape of urine. Hence we find that when blood flows freely to the kidney the urine is secreted freely, but that when the blood supply to the kidney is scanty the urine also is scanty. When the renal nerves going to the kidney are cut, the branches of the renal artery dilate, much blood goes into the kidney, the blood-pressure is raised in the glomeruli, and the flow of urine is copious. If the same nerves be stimulated, the arterial tubes are narrowed and constricted, less blood goes to the kidney, blood-pressure is reduced, and the flow of urine is scanty or may be stopped altogether.

We can now explain, in part at all events, how it is that the activity of the kidney is influenced by the state of the skin. The quantity of blood in the body, being about the same at all times, if a large quantity goes to the skin, as

in warm weather and especially when the skin is active and perspiring, less will go to the kidney, and the secretion of urine will be small. On the other hand, if the blood be largely cut off from the skin, as in cold weather, more blood will be thrown upon the kidney and more urine will be secreted. Thus the skin and the kidneys play into each other's hands in their efforts to get rid of the superfluous water of the body.

But the whole of the urine is not thus secreted, through a sort of filtering process, by the Malpighian capsules. The circulation in the kidney is peculiar, inasmuch as the blood coming from the glomeruli is not sent at once into a vein, but is carried into a second capillary network, wrapped round the tubules. The tubules are lined, as has been stated, by epithelium cells, and these cells, in certain parts of the tubule, especially where these are coiled, are what is called *secreting* cells. That is to say they have the power, by some means which we do not at present fully understand, to take up from the blood, which is flowing in the capillaries wound round the tubules, or rather from the plasma which exudes from those capillaries, and bathes the bases of the cells, certain substances, and to pour these substances into the cavity of the tubule.

And we have evidence that many of the most important constituents of the urine, such as urea, uric acid and others, are thus secreted by the epithelium cells of the tubules, and not simply filtered off by the Malpighian capsules.

We may give two striking facts in support of this view. In some animals the glomeruli of the kidney receive their blood-supply by an artery, which is quite distinct from the vessel which takes blood to the tubules. When the artery supplying the glomeruli is tightly tied, no blood can go to the glomeruli, but *urea is still passed out* from the kidney and must come from the tubules. Again, a certain colouring matter when injected into the blood is excreted in the urine; this colouring matter can easily be

tracked through the kidney and be *seen* to pass through the cells of the convoluted tubules and not through the walls of the glomerular blood-vessels.

The formation of urine is therefore a double process. A great deal of the water, with probably some of the more soluble inorganic salts, passes by the glomeruli, but the urea, the colouring matters and a great many other of the constituents, are thrown into the cavities of the tubules by a peculiar action of the epithelium cells.

6. The History of Urea.—Nitrogen enters the body as protein food and, practically, all of it leaves the body again as urea. Somewhere or other, and by some means or other, the nitrogen while in transit is turned over from the proteins into urea. This change involves the whole nitrogenous metabolism [1] of the body and from its importance merits a short statement of the chief facts which throws some light on the question of where and how urea is formed.

In the first place the urea excreted in the urine is *not made in the kidney* out of some other (antecedent) substance. The activity of the kidney consists entirely in picking out ready made urea from the blood which passes through it and discharging this urea into the channels of the tubules. Hence urea must be made in tissues other than the kidney and finds its way from these into the blood.

Nearly half the weight of the body is made up of muscular tissue, the muscles. These muscles are the seat of active oxidation even when at rest, and this activity is enormously increased at times when they are contracting. There must therefore always be a considerable wear and tear going on in them, and we must suppose that this leads to the formation of waste, of which some should contain nitrogen, since the muscles are chiefly built up of nitrogenous material. But this waste does not come out of the muscle as ready-made urea, neither do we

[1] The word metabolism (μεταβολή = change) is conveniently used to denote the sum total of those chemical changes which take place in living matter, and in virtue of which we speak of it as "living."

know as yet exactly in what form it does leave them. In fact all we know is that the muscles give off nitrogenous waste, that this waste is presumably turned into urea in some other part of the body, and the urea picked out and excreted by the kidneys.

But there is another organ in the body of great size and importance, the liver (p. 207). This organ is the seat of many activities with which we shall deal later on, among which the making of urea out of other substances brought in the blood is not the least important. We also know to a certain extent what these "other substances" are. When we study digestion we shall see that the products of digestion of proteins are nitrogenous, crystalline substances known as **amino-acids.** These are absorbed through the walls of the intestines, carried to the liver in the blood of the portal vein, and in part *converted into urea by the liver.* Moreover there are instances of animals which have survived the functional removal of the liver for several days. In such cases the excretion of urea by the kidney is suspended and at the same time there is an accumulation of ammonia in the blood. As it is known that the liver has the power of converting ammonia into urea it seems clear that a considerable proportion of the urea excreted has ammonia as an antecedent. Whatever its exact antecedents we may regard the urea secreted as coming from two main sources, the waste of the tissues and the superfluous nitrogen of the food which is undergoing digestion in the alimentary canal; the urea derived from tissues is called *endogenous* urea, that derived directly from the food, the antecedents of which have never, therefore, been built into the living substance of the body, is called *exogenous* urea. In both cases the final stage in the formation of urea may be regarded as taking place in the liver.

7. The Structure of the Skin. Nails and Hairs.— That the skin is a source of continual loss to the blood may be proved in various ways. If the whole body of a man, or one of his limbs, be enclosed in a caoutchouc bag,

full of air, it will be found that this air undergoes changes which are similar in kind to those which take place in the air which is inspired into the lungs. That is to say, the air loses oxygen and gains carbonic acid ; it also receives a great quantity of watery vapour, which condenses upon the sides of the bag, and may be drawn off by a properly disposed pipe. Further there is a continual loss of heat taking place from the surface of the body. Of these the loss of watery vapour and of heat are of immense importance, for it is chiefly by means of variations in their amount from time to time that the temperature of the body is kept nearly constant. But before dealing with these activities of the skin we must understand the main facts as to its structure.

The skin consists of two parts, an outer layer or **epidermis**, resting on a deeper layer, the **dermis**. The skin as a whole is connected to the tissues it covers by a layer of loose fibrous connective tissue (see Fig. 28), called subcutaneous tissue. This often contains fat, and is the part which is cut through when an animal is skinned.

The dermis is made up of a dense feltwork of ordinary connective tissue fibres mixed with many elastic fibres and some connective tissue corpuscles (see Lesson XII.). The surface of the dermis is raised up into little hillocks or elevations known as the **papillæ**. Arteries enter the dermis and break up into capillaries which are very close set at its surface and in the papillæ ; thus the dermis is *extremely vascular*. Nerves also run into the dermis, and passing outwards, form a branching layer of fibres at its junction with the epidermis, and from this layer extremely fine nerve fibrils pass out and between the lower cells of the epidermis. In some parts of the body, some of the branches of the nerves run up into the papillæ, where they are connected with special nervous structures such as **tactile corpuscles** and **end bulbs**. But since these are of imnortance solely in connection with the

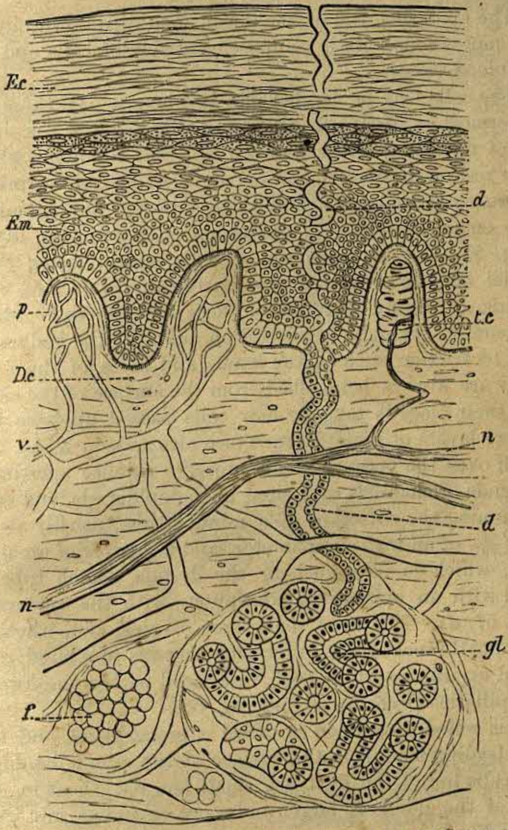

FIG. 57.—DIAGRAM TO SHOW THE STRUCTURE OF THE SKIN.

E.c, epidermis corneous part; *E.m*, epidermis Malpighian part; *D.c* connective tissue of dermis; *p*, papilla; *gl*, sweat gland, the coils of the tube cut across or lengthwise; *d*, its duct; *f*, fat; *v*, blood-vessels; *n*, nerve; *t.c*, tactile corpuscle.

functions of the skin as a sense-organ, they will be described later on (see Lesson VIII.).

The epidermis lies on the dermis and dips down into all its depressions. It is composed entirely of cells and has no blood-vessels.

The cells may be divided into two layers. Of these the innermost or **Malpighian layer** (Fig. 57, *Em.*) is made up of nucleated cells which are tall and columnar where they rest on the dermis, become more rounded and wrinkled as they pass outwards, and then flattened and granular. The outer layer of the epidermis or **corneous layer** (Fig. 57, *Ec.*) is made up of cells which, losing their nuclei become converted into flattened, thin scales, consisting of horny material. These are the cells which become so strongly developed on parts of the body subject to friction such as the hands and soles of the feet. They are always being shed from the surface of the skin, and their place is take by new cells passed up from the deeper layers of the epidermis (see also Lesson XII.).

All over the body the skin presents minute apertures, the ends of channels excavated in the epidermis, and each continuing the direction of a minute tube, usually about 80μ ($\frac{1}{300}$ of an inch) in diameter, and a quarter of an inch long, which is imbedded in the dermis. Each tube is lined with an epithelium continuous with the epidermis (Fig. 57, *d*). The tube sometimes divides, but, whether single or branched, its inner end or ends are blind, and coiled up into a sort of knot, interlaced with a meshwork of capillaries (Fig. 57, *gl*, and Fig. 58).

This coiled-up portion is called a sweat-gland, and the tube leading from it to the surface of the skin is its duct. The cells lining the duct are small and flat, those in the tube of the gland are larger and more columnar, and may be readily stained.

The blood in the capillaries of the gland is separated from the cavity of the sweat-gland only by the thin walls of the capillaries, that of the glandular tube, and its

epithelium, which, taken together, constitute but a very thin pellicle; and the arrangement, though different in detail, is similar in principle to that which obtains in the kidney. In the latter, the vessel makes a coil within the Malpighian capsule, which ends a tubule. Here the perspiratory tubule coils about, and among, the vessels.

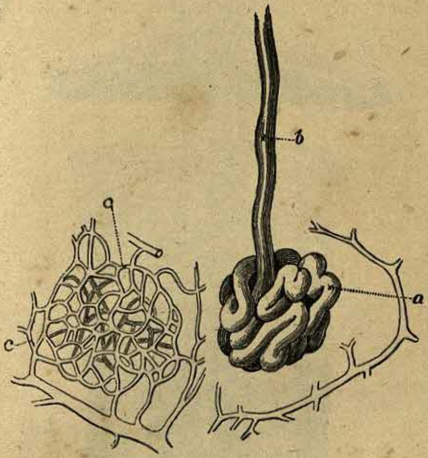

FIG. 58.—COILED END OF A SWEAT-GLAND (Fig. 57, *gl.*), EPITHELIUM NOT SHOWN.

a, the coil; *b*, the duct; *c*, network of capillaries, inside which the gland lies.

In both cases the same result is arrived at—namely, the exposure of the blood to a large, relatively free, surface, on to which certain of its contents transude. In the sweat-gland however there is no filtering apparatus like the Malpighian corpuscle of the kidney, and *the whole of the sweat appears to be secreted into the interior of the tube by the action of the epithelium cells which line it.*

The number of these glands varies in different parts of the body. They are fewest in the back and neck, where

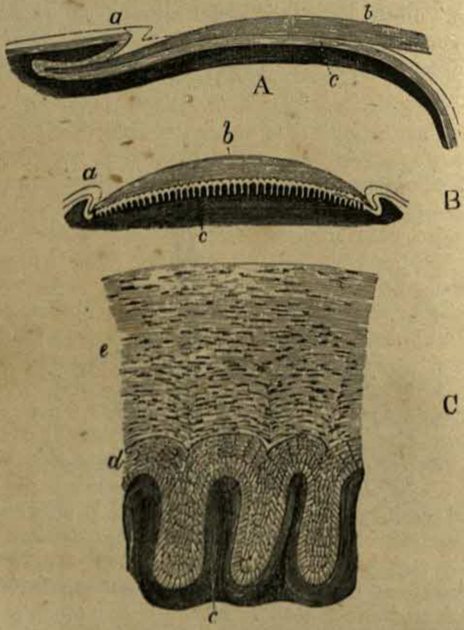

FIG. 59.

A, a longitudinal and vertical section of a nail; *a*, the fold at the base of the nail; *b*, the nail; *c*, the bed of the nail. The figure B is a transverse section of the same—*a*, a small lateral fold of the integument; *b*, nail; *c*, bed of the nail, with its ridges. The figure C is a highly-magnified view of a part of the foregoing—*c*, the ridges; *d*, the deep layers of epidermis; *e*, the horny scales coalesced into nail substance. (Figs. A and B magnified about 4 diameters; Fig. C magnified about 200 diameters.)

their number is not much more than 400 to a square inch. They are more numerous on the skin of the palm and

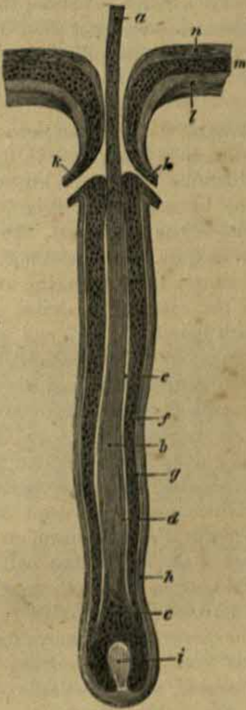

FIG. 60.—A HAIR IN ITS HAIR-SAC.

a, shaft of hair above the skin; *b*, cortical substance of the shaft, the medulla not being visible; *c*, newest portion of hair growing on the papilla (*i*); *d*, cuticle of hair; *e*, cavity of hair-sac; *f*, epidermis (and root-sheaths) of the hair-sac corresponding to that of the integument (*m*); *g*, division between dermis and epidermis; *h*, dermis of hair-sac corresponding to dermis of integument (*l*); *k*, mouths of sebaceous glands; *n*, horny epidermis of integument.

sole, where their apertures follow the ridges visible on the skin, and amount to between two and three thousand on

the square inch. At a rough estimate, the whole integument probably possesses not fewer than from two millions and a quarter to two millions and a half of these tubules, which therefore must possess a very great aggregate secreting power.

In certain regions of the skin the corneous cells of the epidermis are not at once thrown off in flakes, but are at first built up in definite structures known as **nails** and **hairs**, which grow by constant addition to the surfaces by which they adhere to the epidermis. In the case of the nails, the process of growth has no limit, and the nail is kept of one size simply by the wearing away of its oldest or free end. In the case of the hairs, on the contrary, the growth of each hair is limited, and when its term is reached the hair falls out and is replaced by a new hair.

Underneath each **nail** the deep or *dermic* layer of the integument is peculiarly modified to form the **bed of the nail.** It is very vascular, and raised up into numerous parallel ridges, like elongated papillæ (Fig. 59, B, C). The surfaces of all these are covered with growing epidermic cells, which, as they flatten and become converted into horn, form a solid continuous plate, the nail. At the hinder part of the bed of the nail the integument forms a deep fold, from the bottom of which, in like manner, new epidermic cells are added to the base of the nail, which is thus constrained to move forward.

The nail, thus constantly receiving additions from below and from behind, slides forwards over its bed, and projects beyond the end of the finger, where it is worn away or cut off.

A **hair**, like a nail, is composed of horny cells; but instead of being only partially sunk in a fold of the integument it is at first wholly enclosed in a kind of bag, the **hair-sac** or **follicle**, from the bottom of which a **papilla** (Fig. 60, *i*), which answers to a single ridge of the nail, arises. The hair is developed by the conversion into horn, and coalescence into a **shaft**, of the superficial epidermic

cells coating the papilla. These coalesced and cornified cells being continually replaced by new growths from below, which undergo the same metamorphosis, the shaft of the hair is thrust out until it attains the full length natural to it. Its base then ceases to grow, and the old papilla and sac die away, but not before a new sac and papilla have been formed by budding from the sides of the old one. These give rise to a new hair. The shaft of a hair of the head consists of a central pith, or **medullary** matter, of a loose and open texture, which sometimes contains air; of a **cortical** substance sur-

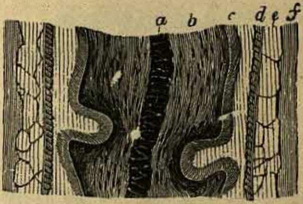

FIG. 61.—PART OF THE SHAFT OF A HAIR INCLOSED WITHIN ITS ROOT-SHEATHS AND TREATED WITH CAUSTIC SODA, WHICH HAS CAUSED THE SHAFT TO BECOME DISTORTED.

a, medulla; *b*, cortical substance; *c*, cuticle of the shaft; from *d* to *f*. the root-sheaths, in section. (Magnified about 200 diameters.)

rounding this, made up of coalesced elongated horny cells; and of an outer **cuticle** composed of flat horny plates, arranged transversely round the shaft, so as to overlap one another by their outer edges, like tiles on the roof of a house. The superficial epidermic cells of the hair-sac also coalesce by their edges, and become converted into **root-sheaths**, which embrace the root of the hair, and usually come away with it when it is plucked out.

The sebaceous glands are small glands whose duct opens into the follicle of a hair. They form a fatty secretion which lubricates the hairs.

8. The Composition and Quantity of Sweat.—The sweat glands have the function of forming a fluid, the sweat, which is passed out on to the surface of the body. This fluid is composed chiefly of water containing a small amount (1–2 per cent.) of solid matter in solution, chiefly sodium chloride.

In its normal state the sweat, as poured out from the proper sweat-glands, is alkaline; but ordinarily, as it collects upon the skin, it is mixed with the fatty secretion of the *sebaceous glands*, and then is frequently acid. In addition it contains scales of the external layers of the epidermis, which are constantly being shed.

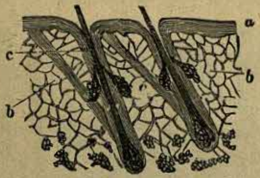

FIG. 62.—SECTION OF THE SKIN SHOWING THE ROOTS OF THE HAIRS AND THE SEBACEOUS GLANDS.

a, epidermis; *b*, muscle of *c* the hair sheath, on the left hand.

Under ordinary conditions the sweat is evaporated from the surface of the skin as fast as it is secreted; in this case it is frequently spoken of as *insensible* perspiration. But when violent exercise is taken, or under some kind of mental emotion, or when the body is exposed to a hot and moist atmosphere, the sweat is secreted faster than it evaporates: the perspiration then becomes *sensible*, that is it appears in the form of scattered drops on the surface of the body.

The quantity of sweat, or sensible perspiration, and also the total amount of both sensible and insensible perspiration, vary immensely, according to the temperature and other conditions of the air, and according to the

state of the blood and of the nervous system. It is estimated that, as a general rule, the quantity of water excreted by the skin is about double that given out by the lungs in the same time.

The amount of matter which may be lost by perspiration under certain circumstances, is very remarkable. Heat and severe labour, combined, may reduce the weight of a man two or three pounds in an hour, by means of the cutaneous perspiration alone ; and there is some reason to believe that the total amount of solids which are eliminated by profuse sweating may be considerable.

9. A Comparison of the Lungs, Kidneys, and Skin.—It will now be instructive to compare together in more detail than has been done in the first Lesson (p. 24), the three great organs—lungs, kidneys, and skin—which have been described.

In ultimate anatomical analysis, each of these organs consists of a moist animal membrane separating the blood from the atmosphere.

Water, carbonic acid, and solid matter pass out from the blood through the animal membrane in each organ, and constitute its secretion or excretion ; but the three organs differ in the absolute and relative amounts of the constituents the escape of which they permit.

Taken by weight, water is the predominant excretion in all three ; most solid matter is given off by the kidneys ; most gaseous matter by the lungs.

The skin partakes of the nature of both lungs and kidneys, seeing that it absorbs oxygen and exhales carbonic acid and water, like the former, while it excretes organic and saline matter in solution, like the latter ; but the skin is more closely related to the kidneys than to the lungs. Hence, as has been already said, when the free action of the skin is interrupted, its work is usually thrown upon the kidneys, and *vice versa.* In hot weather, when the excretion by the skin increases, that of the

kidneys diminishes, and the reverse is observed in cold weather.

This power of mutual substitution, however, only goes a little way; for if the kidneys be extirpated, or their functions much interfered with, death ensues, however active the skin may be. And, on the other hand, if the skin be covered with an impenetrable varnish, the temperature of the body rapidly falls, and death takes place, though the lungs and kidneys remain active.

10. The Secretion of Sweat and its Nervous Control.—In analysing the process by which the perspiration is eliminated from the body, it must be recollected, in the first place, that the skin, even if there were no glandular structures connected with it, would be in the position of a moderately thick, permeable membrane, interposed between a hot fluid, the blood, and the atmosphere. Even in hot climates the air is, usually, far from being completely saturated with watery vapour, and in temperate climates it ceases to be so saturated the moment it comes into contact with the skin, the temperature of which is, ordinarily, twenty or thirty degrees above its own.

A bladder exhibits no sensible pores; but if a bladder be filled with water and suspended in the air, the water will gradually ooze through the walls of the bladder, and disappear by evaporation. Now, in its relation to the blood, the skin is such a bladder full of hot fluid.

Thus, perspiration to a certain amount, must always be going on through the substance of the integument, but probably not to any great extent; though what the amount of this perspiration may be cannot be accurately ascertained, because it is entirely masked by the secretion from the sweat-glands.

When from any ordinary cause an increased formation of sweat takes place, two things usually happen. The small arteries which supply the capillary network surrounding the coiled tube of the sweat-gland dilate

and there is an increased flow of blood through these capillaries. At the same time the cells of the glands begin to pour out an increased quantity of fluid, in other words they begin to secrete. The first of the above two results is brought about by a *lessening of the vaso-constrictor impulses* which had previously been keeping the arteries constricted (see p. 68). But what, on the other hand, is the cause of the simultaneously increased activity of the sweat-glands? Do they simply secrete faster because of the increased supply of blood brought to them? Or is it because their cells are urged on to greater activity by special nervous impulses sent to them? The latter is the real explanation of the increased activity of the cells, as shown by the following facts.

It is possible to obtain an increased secretion of sweat by the stimulation of nerves in parts of an animal's body from which the blood supply has been previously cut off. Again, certain drugs may lead to sweating without at the same time producing any vascular changes, and the same effect is often observed in sweating which results from mental emotions and in the "cold sweats" of a disease such as phthisis. The nerves which can thus make the cells of the sweat-glands become more active may be called **secretory nerves.** They appear to be connected with a centre in the central nervous system, and by this means sweating may be brought about reflexly, as when placing mustard in the mouth causes the face to sweat. The possibility of such reflex stimulation of the sweat-glands acquires an extraordinary importance, as we shall see when we come to consider the means by which the temperature of the body is regulated (p. 203).

11. Animal Heat: its Production and Distribution.—It has been seen that heat is being constantly given off from the skin and from the air-passages; and everything that passes from the body carries away with it, in like manner, a certain quantity of heat. Furthermore, the surface of the body is much more exposed to

cold than its interior. Nevertheless, the temperature of the body is in health maintained very evenly, at all times and in all parts, within the range of two degrees or even less on either side of 37° C. (98·6° Fahrenheit).

This is the result of three conditions :—the first, that heat is constantly being generated in the body; the second, that it is as constantly being distributed through the body; the third, that it is subject to incessant regulation as regards both loss and production.

Heat is generated whenever oxidation takes place. As we have seen, the tissues all over the body, muscle, brain-substance, gland-cells and the like, are continually undergoing oxidation. The living substance of the tissue, built up out of the complex proteins, fats, and carbohydrates, and thus even still more complex than these, is, by means of the oxygen brought by the arterial blood, oxidised, and broken down into simpler more oxidised bodies, which are eventually reduced to urea, carbonic acid, and water. Wherever life is being manifested these oxidative changes are going on, more energetically in some places, in some tissues, and in some organs, than in others. Hence every capillary vessel and every extra-vascular islet of tissue is really a small fireplace in which heat is being evolved, in proportion to the activity of the chemical changes which are going on.

The chief seat of this heat production is undoubtedly in the muscles; for, as already pointed out, they make up about half the body-weight, and are carrying on an active oxidation even while at rest. This gives rise to heat, and when a muscle enters into a state of contracting activity, the heat production becomes so rapid as to produce an actual measurable rise of its temperature. After the muscles we may regard the liver and the other secreting glands as the next great heat-producing organs of the body.

But as the vital activities of different parts of the

body, and of the whole body, at different times, are very different; and as some parts of the body are so situated as to lose their heat by radiation and conduction much more easily than others, the temperature of the body would be very unequal in its different parts, and at different times, were it not for the arrangement by which the heat is distributed and regulated.

Whatever oxidation occurs in any part, raises the temperature of the blood which is in that part at the time, to a proportional extent. But this blood is swiftly hurried away into other regions of the body, and rapidly gives up its excess heat to them. On the other hand, the blood which, by being carried to the vessels in the skin on the surface of the body begins to have its temperature lowered by evaporation, radiation, and conduction, is hurried away, before it has time to get thoroughly cooled, into the deeper organs; and in them it becomes warm by contact, as well as by the oxidating processes there going on. Thus the blood-vessels and their contents may be compared to a system of hot-water pipes, through which the warm water is kept constantly circulating by a pump; while it is heated not by a great central boiler as usual, but by a multitude of minute gas jets, disposed beneath the pipes not evenly, but more here and fewer there. It is obvious that, however much greater might be the heat applied to one part of the system of pipes than to another, the general temperature of the water would be even throughout, if it were kept moving with sufficient quickness by the pump. In this way, then, the temperature of the body is kept *uniform* in its several parts.

12. Regulation of Body-temperature by Altered Loss of Heat.—If a system such as we have just imagined were entirely composed of closed pipes, the temperature of the water might be raised to any extent by the gas jets. On the other hand, it might be kept down to any required degree by causing a larger, or smaller, portion of the pipes to be wetted with water,

which should be able to evaporate freely—as, for example, by wrapping them in wet cloths. And the greater the quantity of water thus evaporated, the lower would be the temperature of the whole apparatus.

Now, the regulation of the temperature of the human body is chiefly effected on this principle. The vessels are closed pipes, but a great number of them are inclosed in the skin and in the mucous membrane of the air-passages, which are, in a physical sense, wet cloths freely exposed to the air. It is the evaporation from these which exercises a more important influence than any other condition upon the regulation of the temperature of the blood, and, consequently, of the body.

But, as a further nicety of adjustment, the wetness of the regulator is itself determined, through the aid of the nervous system, by the temperature of the body. The sweat-glands, as we have seen, may be made to secrete by impulses reaching them along certain nerves coming from a centre in the central nervous system. This centre is itself connected by other nerves with the skin, and the ends of these cutaneous nerves are so constituted that they are stimulated by heat applied to the skin. When the body is exposed to a high temperature (and the same occurs when a part only of the body is heated), these cutaneous nerves convey impulses to the central nervous system, from which other impulses are then sent out along the secretory nerves to the sweat-glands and cause them to pour forth a copious secretion on to the skin; and when the temperature falls, the glands cease to act. Moreover, in this work of secreting sweat, the sweat-glands are assisted by corresponding changes in the blood-vessels of the skin. It has been stated (see p. 68) that the small arteries of the body may be sometimes narrowed or constricted, and sometimes widened or dilated. Now the condition of the small arteries, whether they are constricted or dilated, depends, as we have also seen, upon the action of certain nerves (vaso-motor nerves).

And it appears that when the body is exposed to a high temperature these nerves are so affected as to lead to a dilation of small arteries of the skin; but when these are dilated the capillaries and small veins in which they end become much fuller of blood, and from these filled and swollen capillaries much more nutritive matter passes through the capillary walls to the sweat-glands, so that these have more abundant material from which to manufacture sweat. On the other hand, when the body is lowered in temperature the vaso-motor nerves are so affected that the small arteries of the skin are constricted; hence less blood enters the capillaries of the skin, and less material is brought to the sweat-glands.

Thus when the temperature is raised two things happen, both brought about by the nervous system. In the first place, the arteries of the skin are widened so that a much larger proportion of the total blood of the body is carried to the surface of the skin and there becomes cooled: and, secondly, this cooling process is greatly helped by the increased evaporation resulting from the increased action of the sweat-glands, whose activity is further favoured by the presence in the skin of so much blood. Conversely when the temperature is lowered, less of the blood is brought to the skin, and more of the blood circulates through the deeper, hotter parts of the body, and the sweat-glands cease their work (this quiescence of theirs being in turn favoured by the lessened blood-supply); hence the evaporation is largely diminished, and thus the blood is much less cooled.

Hence it is that, so long as the surface of the body perspires freely, and the air passages are abundantly moist, a man may remain with impunity, for a considerable time, in an oven in which meat is being cooked. The heat of the air is expended in converting this superabundant perspiration into vapour, and the temperature of the man's blood is hardly raised.

13. Regulation of Body-temperature by Altered

Production of Heat.—The temperature of the body is kept constant by that carefully adjusted variation in loss of heat from its surface which has been described in the preceding section. But now we may point out that there is another way by which this constancy *might* be attained, namely by *altering the production of heat* taking place in the body, in correspondence to the changes of the surrounding temperature ; just as the temperature of a room may be regulated by putting out or increasing the fire as well as by opening or closing its windows. The question thus raised is very interesting, but it is also very abstruse, and we must not do more than just touch upon it.

All oxidation in the body involves the consumption of oxygen, the production of carbonic acid and the generation of an exactly corresponding quantity of heat. We may therefore take the difference in the amount of oxygen used up (and of carbonic acid produced) at different times as a measure of the amount of heat being produced in the body during the same periods. Working in this way it is found that when a warm-blooded animal is exposed to cold, as when it is put into a chamber which is cooled, it uses up more oxygen and gives off more carbonic acid than when put into a warm chamber. But this can only mean that in the cooler surroundings the animal makes more heat than when the surroundings are warm. Perhaps the most evident instance of increased heat production, in response to unusual heat loss, is that of shivering. When, owing to lowering of the external temperature or to insufficient clothing, the ordinary sources of heat fail to maintain the temperature of the body, impulses pass from the brain to the muscles which cause them to contract rhythmically. In other words the subject shivers. Muscular contraction, as we have already seen, involves oxidation (see p. 203), and oxidation is accompanied by heat production. Again we may point out, as tending to the same conclusion, that our desire for food is greater, on the whole, in the cooler winter time than in the

warmer summer; and all food is, sooner or later, oxidised in the body and during this oxidation gives rise to heat. There are reasons for supposing that within certain limits altered production of heat plays a part in keeping the temperature of the body constant.

All the functions of the body which we have so far studied have been seen to be under the guidance of nervous impulses. We may therefore suppose that the production of heat will be no exception to the rule, and indeed there are reasons, based largely on experiment and partly on the phenomena of certain diseases, which justify this view. More than this we must not say.

14. **The Temperature of Fever.**—The condition to which the name of fever is given is characterised essentially by the temperature of the body being higher than is usual in health. Thus it may rise to as much as 41° C. (105·8° F.) or occasionally even above this point, and there has been much dispute as to how this high temperature arises. By many it is regarded simply as the outcome of a disturbance of the mechanism by which heat is lost to the body, some diminution in loss of heat leading naturally to a rise of temperature; and probably, this is the most common cause of the rise of temperature. But on the other hand direct measurement shows that a fevered person often *gives off more heat than usual* and at the same time uses up more oxygen and produces more carbonic acid and urea than is usual. In such cases there is no doubt that the abnormally high temperature is largely due to an over-production of heat.

15. **The Liver.**—The liver is a constant source both of loss, and, in a sense, of gain, to the blood which passes through it. It gives rise to loss, because it secretes a peculiar fluid, the **bile**, from the blood, and throws that fluid into the intestine. It is also in another way a source of loss because it elaborates from the blood passing through it a substance called **glycogen**, which is stored up sometimes in large, sometimes in small, quantities in

the cells of the liver. This latter loss, however, is only temporary, and may sooner or later be converted into a gain, for this glycogen very readily passes into sugar, and either in that form or in some other way is carried off by the blood. In this respect, therefore, there is a gain to the blood of kind or quality though not of quantity of material.

The liver is the largest glandular organ in the body, ordinarily weighing about 1,400–1,700 grammes (fifty or sixty ounces). It is a broad, dark, red-coloured organ, which lies on the right side of the body, immediately below

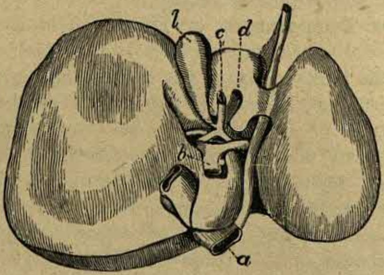

FIG. 63.—THE LIVER TURNED UP AND VIEWED FROM BELOW.

a, vena cava; *b*, vena portæ; *c*, bile duct; *d*, hepatic artery; *l*, gall-bladder. The termination of the hepatic vein in the vena cava is not seen, being covered by the piece of the vena cava.

the diaphragm, with which its upper surface is in contact, while its lower surface touches the intestines and the right kidney.

The liver is invested by a coat of peritoneum, which keeps it in place. It is flattened from above downwards and convex and smooth above, where it fits into the concavity of the lower surface of the diaphragm. Flat and irregular below (Fig. 63), it is thick behind, but ends in a thin edge in front.

Viewed from below, as in Fig. 63, the inferior vena

cava, *a*, is seen to traverse a notch in the hinder edge of the liver as it passes from the abdomen to the thorax. At *b* the trunk of the **vena portæ** is observed dividing into the chief branches which enter into, and ramify through, the substance of the organ. At *d*, the **hepatic artery**, coming almost directly from the aorta, similarly divides, enters the liver, and ramifies through it. At *c* is the single trunk of the duct, called the **hepatic duct**, which conveys away the bile brought to it by its right and left branches from the liver. Opening into the hepatic duct is seen the duct of a large oval sac, *l*, the **gall-bladder**. The duct is smaller than the artery, and the artery than the portal vein.

The liver consists of two chief **lobes** of which the right is much larger than the left. Externally the lobes are covered with a layer of connective tissue forming its **capsule**, and a quantity of connective tissue forms a thick sheath for the vena portæ, hepatic artery and bile-duct, as these plunge into the liver. This sheath accompanies the vessels as they ramify into the liver and finally forms a number of partitions, continuous with the capsule on the outside, which divide each lobe into a very large number of smaller divisions called **lobules**. These partitions are much thicker and more conspicuous in some animals, such as the pig, than they are in others, such as the rabbit; in the former it is very easy to see on the outside of the liver the outlines of the lobules; in the latter it is not so easy. The lobules are about $\frac{1}{10}$ of an inch in diameter and are thus visible to the naked eye. Each lobule is made up of a mass of cells, the **hepatic cells**, which lie in the meshes of a close-set network of blood capillaries. These capillaries radiate from a small blood-vessel which runs down the centre of each lobule towards its base; this central blood-vessel is called the **intralobular vein** (Fig. 64, *A*, *H.V.*), and, passing out of the lobule at its base, runs into a branch of that great vein, the **hepatic vein**, which carries the blood away from the

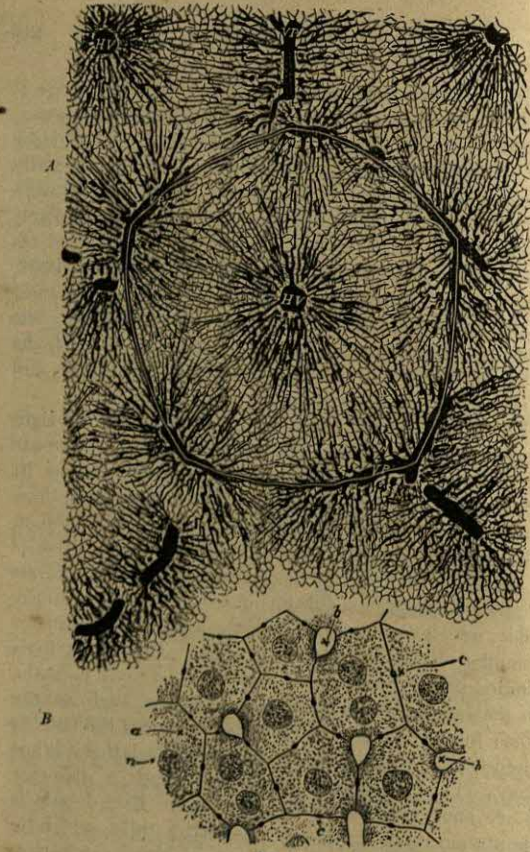

FIG. 64.

A. Section of partially injected liver magnified. The artificial white line is introduced to mark the limits of a lobule. *V.P*, branches of portal vein breaking up into capillaries, which run towards the centre of the lobule, and join *H.V*, the intralobular branch of the hepatic vein. The outline of the liver cells are seen as a fine network of lines throughout the whole lobule.

B. Portion of lobule very highly magnified. *a*, liver cell with *n*, nucleus (two are often present); *b*, capillaries cut across; *c*, minute biliary passages between the cells, injected with colouring matter.

liver. In this way each lobule comes to be seated by its base on a branch of the hepatic vein (Fig. 65, *H.V.*).

If the branches of the hepatic artery, the portal vein, and the bile duct be traced into the substance of the liver, they will be found to accompany one another, and to

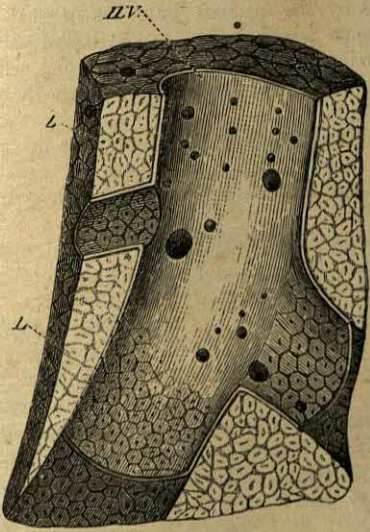

FIG. 65.—A SECTION OF PART OF THE LIVER TO SHOW

H.V, a branch of the hepatic vein, with *L*, the lobules or acini of the liver, seated upon its walls, and sending their intralobular veins into it.

branch out and subdivide, becoming smaller and smaller. At length the ultimate branches of the portal vein (Fig. 64, *V.P.*) reach the outer surfaces of the lobules, and passing round and between them are known as the **interlobular veins.** These veins pour their blood into the network of capillaries which permeate each lobule. The branches

of the hepatic artery follow a course parallel to that of the portal vein and finally, reaching the surface of a lobule, pour the blood they carry into the lobular capillaries.

Thus the venous blood of the portal vein and the arterial blood of the hepatic artery reach the surfaces of the lobules by the ultimate branches of that vein and artery, become mixed in the capillaries of each lobule, and are carried off by its *intralobular* veinlet, which pours its contents into one of the branches of the hepatic vein. These branches, joining together, form larger and larger trunks, which at length reach the hinder margin of the liver, and finally open into the *vena cava inferior*, where it passes upwards in contact with that part of the organ.

Thus the blood with which the liver is supplied is a mixture of arterial and venous blood: the former brought by the hepatic artery directly from the aorta, the latter by the portal vein from the capillaries of the stomach, intestines, pancreas, and spleen.

In the lobules themselves all the meshes of the blood-vessels are occupied by the *liver cells*, or *hepatic cells*. These are many-sided minute bodies, each about 25μ ($\frac{1}{1000}$th of an inch) in diameter, possessing a nucleus in its interior, and frequently having larger and smaller granules of fatty matter distributed through its substance (Fig. 64, *B*, *a*). It is in the liver cells that the active powers of the liver reside.

The smaller branches of the hepatic duct, lined by an epithelium, which is continuous with that of the main duct, and thence with that of the intestines, into which the main duct opens, may be traced to the very surface of the lobules, where they seem to end abruptly (Fig. 66). But, upon closer examination, it is found that they communicate with a network of minute passages passing between the hepatic cells, and traversing the lobule in the intervals left by the capillaries (Fig. 64, *B*, *c*). These

minute passages are the **bile canaliculi**. The bile manufactured by the hepatic cells finds its way first into these minute passages, and from them into the ducts.

16. The Work of the Liver. Its Glycogenic Function.—The work of the liver, and this, as has been said, is carried out by the hepatic cells, may be considered as consisting of two kinds.

On the one hand, the hepatic cells are continually en-

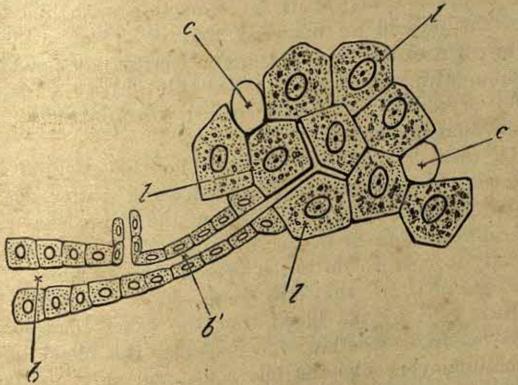

FIG. 66.—TERMINATION OF BILE DUCT AT EDGE OF LOBULE (SOMEWHAT DIAGRAMMATIC).

b, small bile duct, becoming still smaller at *b'*, the low, flat epithelium at last suddenly changing into the hepatic cells, *l*, the channel of the bile duct being continued as small passages between the latter. *c*, capillary blood-vessel cut across.

gaged in the manufacture of a complex fluid called bile, which they pour into the minute passages spoken of above, and thence into the branches of the hepatic duct; whence it flows through the duct itself into the intestines, or, when digestion is not going on and the opening of the duct into the intestine is closed, back to the gall-bladder. The materials for this bile are supplied to the

hepatic cells by the blood; hence the secretion of the bile constitutes a loss to the blood.

The total quantity of bile secreted in the twenty-four hours varies, but probably amounts to not less than from two to three pounds. It is a golden yellow, slightly alkaline fluid, of extremely bitter taste, consisting of water with from 15 per cent. to half that quantity of solid matter in solution. We shall deal with the composition of bile and the nature of its constituents when we come to speak of it in connection with digestion. For the present we may say that its colour is due to **bile-pigments**; that it contains certain compounds of sodium with organic acids called **bile-salts**; a remarkable crystalline substance called **cholesterin**; and some inorganic **salts.**

Of these constituents of the bile the essential substances, the bile acids and the colouring matter, are not discoverable in blood which enters the liver; they must therefore be formed in the hepatic cells. How they are exactly formed we do not at present clearly know. The material of which they are composed is brought to the hepatic cells by the blood, but the exact condition of that material—whether, for instance, the blood brings something very like the bile acids, and only needing a slight change to be converted into bile acids; or whether the hepatic cells manufacture the bile acids from the beginning, as it were, out of the common material which the blood brings to the liver as to all other tissues and organs—is not as yet quite determined. There is however but little doubt that the pigment of bile is in some way made out of the hæmoglobin of the red blood-corpuscles. The saline matters and cholesterin, on the other hand, appear to be present in the blood of the portal vein, and may therefore, like the water, be simply taken up by the cells from the blood, and passed on to the bile ducts.

Thus the bile is a continual loss to the blood. But,

besides forming bile, the hepatic cells are concerned in other labours, the result of which can hardly be considered either as a loss or as a gain, since these labours simply consist in manufacturing from the blood and storing up in the hepatic cells substances which, sooner or later, are returned, generally in a changed condition, back into the blood. For instance we have already seen that salts of ammonium carried by the blood to the liver are there converted into urea and are returned as such to the blood.

Again, as we shall presently see, the portal blood is, after a meal, heavily laden with substances, the result of the digestive changes in the alimentary canal. When these substances, carried along in the portal blood, reach the hepatic cells, in the meshes of the lobules, some of them appear to be taken up by those cells and to be stored up in them in a changed condition. In fact, the products of digestion passing along the portal veins suffer (in the liver) a further change, which has been called a secondary digestion. Thus the liver produces a powerful effect on the quality of the blood passing through it, so that the blood in the hepatic vein is very different, especially after a meal, from the blood in the portal vein.

The changes thus effected by the hepatic cells are probably numerous, but they have not been fully worked out, except in one particular case, which is very interesting and deserves special attention.

It is found that the liver of an animal which has been well and regularly fed, when examined immediately after death, contains a considerable quantity of a substance which is very closely allied to starch, consisting of carbon hydrogen, and oxygen in proportions the same as in starch. This substance, which may by proper methods be extracted and preserved as a white powder, is in fact an **animal starch**, and is called **glycogen**. As we shall see, common starch is readily changed by certain

agents into grape sugar, or dextrose, as it should be called; and this glycogen is similarly converted with ease into dextrose. Indeed, if the liver of such an animal as the above, instead of being examined immediately after death, be left in the body, or be placed on one side after removal from the body for some hours before it is examined, a great deal of the glycogen will have disappeared, a quantity of dextrose having taken its place. There seems to be present in the liver some agent capable of converting the glycogen into a special sort of sugar called dextrose and this change is particularly apt to take place if the liver is kept at blood-heat or near that temperature.

Now if, instead of the liver of a well-fed animal, the liver of an animal which has been starved for several days be examined in the same way, very little glycogen indeed will be found in it, and when this liver is left exposed to warmth for some time very little dextrose is found. That is to say, the liver has, in the first case, formed the glycogen and stored it up in itself, out of the food brought to it by the portal blood: in the second case, no food has been brought to the liver from the alimentary canal, no glycogen has been formed, and none stored up. If the liver in the first case be examined microscopically with certain precautions, the glycogen may be seen stored up in the hepatic cells; in the second case little or none can be seen.

The kind of food which best promotes the storing up of glycogen in the liver is one containing starch or sugar; but some glycogen will make its appearance even when an animal is fed on an exclusively protein diet, though not nearly so much as when starch or sugar is given.

It would appear, then, that the hepatic cells can manufacture and store up in themselves the substance glycogen, being able to make it out of even protein matter, but more easily making it out of sugar; for, as we shall see, all the starch which is eaten as food is converted into sugar in the alimentary canal, and reaches the liver as sugar.

There are reasons for thinking that the glycogen, thus deposited and stored up in the liver, is converted into sugar little by little as it is wanted, poured into the hepatic vein, and thus distributed over the body. So that we may regard this remarkable formation of glycogen in the liver as an act by which the blood, when it is over-rich in sugar, as after a meal, stores it up or deposits it in the liver as glycogen ; and then, in the intervals between meals, the liver deals out the stored-up material as sugar back again in driblets to the blood. The loss to the blood therefore, is temporary—no more a real loss than when a man deposits at his banker's some money which he has received until he has need to spend it.

This story of glycogen, important in itself, is also useful as indicating other possible effects of a similar nature which the hepatic cells may bring about on the blood, as it is passing in the meshes of the lobules of the liver from the veinlets of the portal to the veinlets of the hepatic vein.

The contrast between the two types of function exercised by the liver, the secretion of bile down the bile duct and the secretion of sugar into the blood, was emphasised by Claude Bernard, the celebrated French physiologist, who discovered glycogen. The secretion of bile he called an *external* secretion because it passed away along a duct, the secretion of sugar into the blood was termed an *internal* secretion. We shall have to consider other examples of internal secretions and indeed the secretory functions of glands which have no ducts must be confined to the manufacture of such.

17. **The Thyroid Body or Gland.**—This organ consists of two lobes, one lying each side of the trachea just below the larynx and joined across the trachea by a connecting strip of its own tissue. Each lobe is covered with a capsule of connective tissue from which branches pass inwards and divide the interior into rounded spaces or alveoli. Each alveolus is lined by a layer of cubical cells

so as to leave a large central space ; this space in each alveolus is filled with a clear, viscid, often semi-solid fluid. The viscidity of this fluid is due to the presence in it of a substance which in some respects is like the mucin of mucus. This material is known as the *colloid substance* of the thyroid and is remarkable among the various constituents of the body as containing the chemical element *iodine*.

The thyroid gland contributes an internal secretion to the blood the importance of which may be judged from the following circumstances. Children in which the thyroid is deficient present a very painful picture. They develop neither physically nor mentally, at fifteen or twenty years of age they have not advanced further than a normal child of five years old, their stature is as small, their appearance somewhat deformed, and they lack any mental development. They are known as "cretins." If such are made to eat thyroid glands, or extracts of these glands, they at once develop rapidly and in the course of a few years they become normal persons, and remain such so long as they persist with the diet. Perhaps even more remarkable is the fact that, when pieces of thyroid from normal persons are grafted under the skin of cretins, if the grafts establish themselves, the patients develop rapidly into normal individuals.

Disease of the thyroid glands often leads to disorders, strikingly manifest in the skin, but also involving other organs and tissues, especially perhaps the nervous system and thus leading to nervous troubles. Occasionally the degenerations of the tissues take on the form of a change into a mucin-like substance. These troubles may be largely mitigated by administering an extract of the fresh gland or by eating the fresh gland-substance. Goitre is an enlargement of the thyroid ; at one time surgeons removed the gland, but the removal of the gland was found to be followed by the symptoms which we have described.

18. **The Suprarenal Bodies.**—The suprarenal bodies are two in number, and are placed on the upper edge of each kidney. They are enveloped in an outer coat or capsule of connective tissue from which partitions pass into their interior. In this way each suprarenal is divided up into compartments. In the outer or *cortical* part the compartments are long and narrow, and placed with their long axis at right angles to the surface of the organ. In the centre or *medullary* portion the connective tissue forms a somewhat coarse network. The elongated spaces in the cortex are filled with large angular cells, placed in rounded groups immediately next to the capsule, but arranged more in columns towards the central parts of the compartments. The cells which fill the spaces of the medullary network are of irregular shape and usually branched. These cells contain some peculiar substance, of which but little is known beyond the fact that it gives a dark blue or green colour with ferric chloride, and a bright red colour by treatment with oxidising agents.

The functions of the suprarenal bodies are important, although, as yet, but little understood. When they are both removed from an animal, death speedily ensues, accompanied chiefly by a nutritional upset of the skeletal muscles. When diseased in man, a similar defect is observed in the muscles, together with nervous weakness and a characteristic "bronzing" or coloration of the skin. They too contribute an internal secretion to the blood.

Extracts of the *medulla* when injected into the circulation have an extremely marked action in causing a rise of blood-pressure. This is brought about by an extensive constriction of the minute blood-vessels (arterioles) of the body, and is due to the presence in the extract of the crystalline substance known as "**adrenalin.**" For instance, if the ear of the rabbit be carefully observed when a dose of adrenalin is being injected into a vein with a syringe the vessels of the ear will almost disappear

from view and the ear will become pale and cold. This result we have already seen to take place (p. 67) when the cervical sympathetic nerve, which supplies the muscular wrapping of these vessels, is stimulated. Indeed, when we analyse the action of the adrenalin we find that it does actually stimulate the branches of the cervical sympathetic not along the course of the fibres, but at their termination just where they penetrate the muscular fibres. Nor is the action of adrenalin confined to nerve endings of sympathetic fibres going to blood-vessels, but it stimulates the nerve endings of sympathetic fibres generally, whatever their function. It therefore causes acceleration of the heart, secretion of saliva and many other changes.

The amount of adrenalin necessary to produce these effects is very small. In a rabbit a rise of blood-pressure may be obtained by the injection of one millionth of a gramme. The amount of adrenalin injected, therefore, bears about the same proportion to the rabbit as would a drop of water dropped into an express locomotive engine, and this suffices not only to construct every muscular fibre in the vascular system, but to produce a multitude of other effects.

19. **The Thymus Gland.**—This is an organ which lies over the trachea, in the lower part of the neck and behind the sternum at the base of the heart. It is conspicuous at birth but soon begins to waste away, and in the adult is replaced by a small amount of connective tissue and fat. In structure it somewhat resembles a lymphatic gland; thus it has an external capsule from which trabeculæ pass inwards and divide it up into regular compartments or follicles. These follicles are filled with a network of lymphatic connective tissue which is crowded with leucocytes.

Nothing very definite is known of the function or use of this gland.

20. **The Spleen.**—The spleen lies in the abdominal

cavity, slightly below and towards the left side of the stomach and immediately to the left of the tail of the pancreas (Fig. 67). It is an elongated, flattened, red body, abundantly supplied with blood by an artery called the **splenic artery**, which proceeds almost directly from the aorta. The blood which has traversed the spleen is collected by the **splenic vein**, and is carried by it to the portal vein, and so to the liver. The spleen is covered

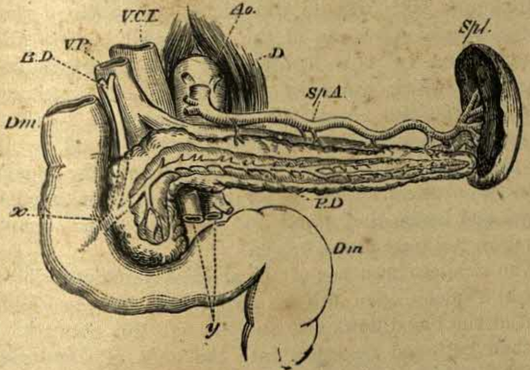

Fig. 67.

The spleen (*Spl.*) with the splenic artery (*Sp.A.*). Below this is seen the splenic vein running to help to form the vena portæ (*V.P.*). *Ao*, the aorta; *D*, a pillar of the diaphragm; *P.D.* the pancreatic duct exposed by dissection in the substance of the pancreas; *Dm.* the duodenum; *B.D*, the biliary duct uniting with the pancreatic duct into the common duct, *x*; *y*, the intestinal vessels.

by a capsular sheath of connective tissue mixed with a good deal of elastic tissue and in some animals a great deal of unstriated muscle fibres. Somewhat in the same way as in a lymphatic gland (p. 89) this capsule sends branching projections or **trabeculæ** inwards which divide the organ up into a number of irregular spaces, and these spaces are filled with a mass of spongy tissue called the **spleen-pulp**. The pulp is traversed by a network of branching cells whose processes are somewhat

flattened and join on to the processes of neighbouring cells. The meshes of this network are occupied by red blood-corpuscles, by colourless corpuscles closely similar to those of lymph, and by other kinds of cells peculiar to the spleen. Some of the latter resemble a colourless corpuscle of blood, in that they can perform amœboid movements, but they are larger and contain in their substance red corpuscles in various stages of disintegration.

A section of the spleen shows a dark red spongy mass dotted over with minute whitish spots. Each of these last is a section of one of the spheroidal bodies called **corpuscles of the spleen,** or **Malpighian corpuscles,** which are scattered through its substance. These corpuscles consist of little masses of lymphoid or adenoid tissue, very similar to that found in the lymphatic glands (p. 90), which surround the smaller branches of the arteries. They are crowded with leucocytes, and hence they stand out as white specks against the dark red pulp of the spleen.

The smallest branches of the arteries which carry blood into the spleen, open into the network of the spleen-pulp, so that the blood flows into and through this network; it is then gathered up again into the ends of tiny veins, which similarly open into the spleen-pulp, and carry the blood away into the splenic vein.

We are still very much in the dark as to the functions of the spleen; they are without doubt of some importance; but on the other hand the spleen may be permanently removed from the body without producing any obvious derangement of its working.

The elasticity of the splenic tissue allows the organ to be readily distended with blood, and enables it to return to its former size after distention. It appears to change its dimensions with the state of the abdominal viscera, attaining its largest size about six hours after a full meal, and falling to its minimum bulk six or seven hours later, if no further supply of food be taken.

The blood of the splenic vein is found to contain proportionally fewer red corpuscles, but more colourless corpuscles, than in the splenic artery; and it has been supposed that the spleen is one of those parts of the economy in which, on the one hand, colourless corpuscles of the blood are produced, and, on the other, red corpuscles die and are broken up.

21. **The Pituitary Body** is a small structure underneath the brain from which its posterior lobe is developed; the anterior lobe and a portion joining the two lobes together is developed from the epithelium of the mouth.

The functions of the pituitary body are obscure, but so far as they are known they are striking enough. Enlargement of the anterior portion is associated with a diseased condition in which many of the bones grow to an abnormal size. Injection of extracts of the posterior part, on the other hand, produces results somewhat similar to, but not quite the same as, injection of adrenalin.

LESSON VI

THE FUNCTION OF ALIMENTATION

PART I.—DIGESTION AND ABSORPTION

1. Waste made good by Food.—We explained in the first Lesson that a living active man is always expending energy in the form of the mechanical (muscular) work he performs and of the heat he gives off by his skin and lungs. Further, we pointed out that the source from which the energy is derived lies in that constant oxidational breaking down of the tissues which results from their being supplied with oxygen, introduced into the body by the lungs. And further, it was shown that the above processes result in a waste of substance corresponding exactly to the amount of energy expended. If the man's activity is to continue from day to day, this continual waste of substance must be made good. Now the only channel, except the lungs, by which altogether new material is introduced into the body, is the alimentary canal, and we may use the word alimentation to denote the sum total of its operations in this connection. These fall naturally under three heads, viz. the *introduction* of food as new material; the reduction of this food by *digestion* to a condition such that it can pass through the delicate structures which form the walls of the vessels of the alimentary canal; and *absorption*, or the processes by which the digested material is passed from the cavity of the canal into the blood-vessels and lymphatics by

which it is then distributed over the body. We may therefore most suitably begin by learning something of the nature and composition of that "new material" which we introduce into the body as food.

2. Food and Food-stuffs.—Every one is familiar with the meaning of the term **food**, as exemplified by bread, meat, potatoes, milk, etc. None of these substances, however, is made up of one kind of material; but when analysed it is found that they all consist of varying amounts of a few substances, and to these the name of **food-stuffs** is given.

Food-stuffs are classified under four heads, (1) **Proteins**, (2) **Fats**, (3) **Carbohydrates**, (4) **Salts** (mineral matter) and **Water**. They may further be divided into two distinct groups:—the **nitrogenous** and the **non-nitrogenous**. The proteins alone contain nitrogen and thus form one group by themselves; the other food-stuffs are all non-nitrogenous. Further, the first three classes, as being compounds of carbon, are known as **organic** compounds, while the salts and water are **inorganic**. They may therefore be tabulated as follows:—

Organic		Inorganic
(Nitrogenous)	(Non-nitrogenous)	(Non-nitrogenous)
Proteins	*Fats*	*Salts*
	Carbohydrates	*Water*

A. Nitrogenous Food-Stuffs.

Proteins.—These are composed of the four elements carbon, oxygen, hydrogen and nitrogen united with small amounts of sulphur (see p. 108). Under this head come the **albumin** of the white of egg, and blood-serum; the **casein** of milk and cheese; the

gluten of flour and other cereals; the **myosin** of lean meat (muscle); the **globulins** of blood and of the yolk of an egg and the **fibrin** of blood.

Gelatin, the basis of connective tissue fibres, contains, like protein, carbon, hydrogen, nitrogen, and oxygen in the proportions in which they occur in protein, and may be regarded as an outlying member of this group. But gelatin contains no sulphur and cannot entirely replace protein in food.

B. NON-NITROGENOUS FOOD-STUFFS.

(i) **Fats.**—These are composed of carbon, oxygen, and hydrogen only, and contain less oxygen than would form water if united to the hydrogen they contain. **Butter** and all animal and vegetable **oils** come under this head.

(ii) **Carbohydrates.**—These are substances which also consist of carbon, oxygen, and hydrogen only, but in them the oxygen is present in an amount which would just suffice to form water *if* it were united to their hydrogen. This group includes **starch**, as in flour or potatoes; ordinary **cane-sugar** or **beet-sugar**, and other sugars such as **dextrose** and **milk-sugar**; also **cellulose** from all vegetable tissues.

(iii) **Salts** and **Water.**—Water is present in all foods, and salts in most of them such as meat, eggs, milk, and cheese. The salts are chiefly the phosphates, chlorides, and carbonates of sodium, potassium and calcium, and some salts of iron.

All food is made up of these food-stuffs, but the amount of each present in different foods varies greatly. Thus meat is chiefly protein, but ordinarily contains a good deal of fat; bread contains a great deal of carbohydrates, but also some protein and a little fat. Only the fats and oils may be regarded as composed of nearly pure material. The composition of the chief foods is important and has been carefully determined; but to this we shall return when we come to study their respective influence on the body as a whole.

3. **The purpose and means of Digestion.**—All food-stuffs being thus proteins, fats, carbohydrates, or mineral matters, pure or mixed up with other substances, the whole purpose of the alimentary apparatus is in the first place to separate these proteins, &c., from the in-nutritious residue, if there be any, and to reduce them to a condition of fine subdivision and ultimately to one of solution, in order that they may make their way through the delicate structures which form the walls of the vessels of the alimentary canal. In the next place this mechanical and physical change must be accompanied by chemical changes whereby the food-stuffs are brought into such a condition that when they reach the tissues the latter can take them up or *assimilate* them.

To these ends food is taken into the mouth and masticated, is mixed with saliva, is swallowed, undergoes gastric digestion, passes into the intestine, and is subjected to the action of the secretions of the liver and pancreas with which it there becomes mixed; and, finally, after the more or less complete extraction of the nutritive constituents, the residue, mixed up with certain secretions of the intestines, leaves the body as the **fæces**.

The actual digestive changes of food are brought about chiefly by the action of fluids secreted by glands whose ducts pour their secretions into the cavity of the alimentary canal. These glands are essentially groups of cells supplied with nerves and blood-vessels; but the arrangement of these cells may be simple or complicated, as in the types shown in Fig. 68.

Thus the glands of the walls of the intestines are tubular (1). Those in the walls of the stomach are also tubular but divided into two or more parts at their inner end (2). The salivary glands and the pancreas are more complicated; their ducts divide and subdivide into multitudes of smaller tubes, each of which ends in a dilatation in which the secreting cells lie (6). These dilatations, attached to the branched ducts, somewhat resemble a

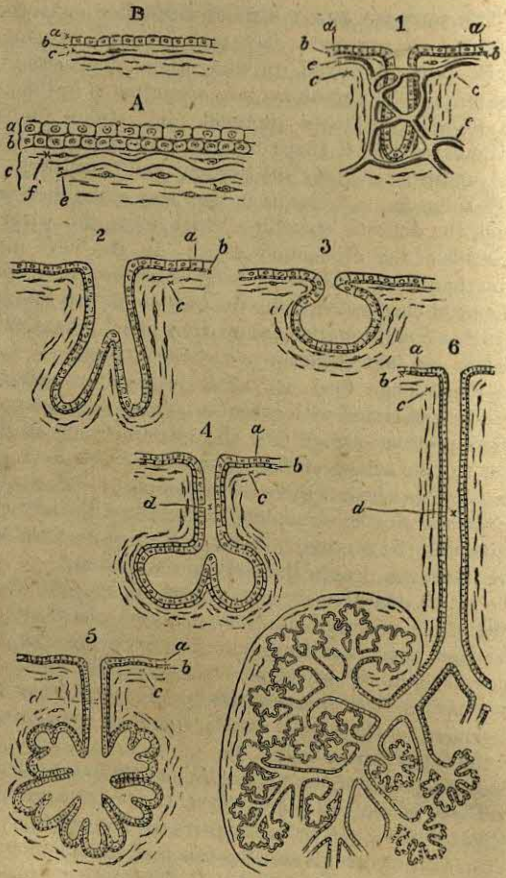

FIG. 68.—A DIAGRAM TO ILLUSTRATE THE STRUCTURE OF GLANDS.

A. Typical structure of the mucous membrane. *a*, an upper, and *b* a lower, layer of epithelium cells; *c*, the dermis with *e* a blood-vessel, and *f*, connective tissue corpuscles.

bunch of grapes, whence glands of this type are called *racemose*.

4. Mastication and Swallowing.—The cavity of the mouth is a chamber with a fixed roof, formed by the **hard palate** (Fig. 69, *l*), and with a movable floor, constituted by the lower jaw, and the tongue (*k*), which fills up the space between the two branches of the jaw. Arching round the margins of the upper and the lower jaws are the thirty-two teeth, sixteen above and sixteen below, and external to these, the closure of the cavity of the mouth is completed by the cheeks at the sides, and by the lips in front.

When the mouth is shut the back of the tongue comes into close contact with the palate; and, where the hard palate ends, the communication between the mouth and the back of the throat is still further impeded by a sort of fleshy curtain—the **soft palate** or **velum**—the middle of which is produced into a prolongation, the **uvula** (*f*), while its sides, skirting the sides of the passage, or **fauces**, form double muscular pillars, which are termed the *pillars of the fauces*. Between these the **tonsils** are situated, one on each side.

The velum with its uvula comes into contact below with the upper part of the back of the tongue, and with a sort of gristly, lid-like process connected with its base, the **epiglottis** (*e*).

Behind the partition thus formed lies the cavity of the **pharynx**, which may be described as a funnel-shaped bag with muscular walls, the upper margins of the slanting, wide end of which are attached to the base of the skull,

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B. The same, with only one layer of cells, *a*, and *b*, the so-called basement membrane between the epithelium *a*, and dermis *c*.
1. A simple tubular gland.
2. A tubular gland bifid at its base. In this and succeeding figures the blood-vessels are omitted.
3. A simple saccular gland.
4. A divided saccular gland, with a duct, *d*.
5. A similar gland still more divided.
6. A racemose gland part only being drawn.

while the lateral margins are continuous with the sides, and the lower with the floor, of the mouth. The narrow

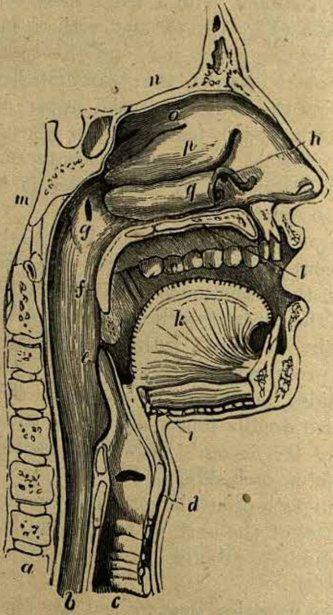

FIG. 69.—A SECTION OF THE MOUTH AND NOSE TAKEN VERTICALLY, A LITTLE TO THE LEFT OF THE MIDDLE LINE.

a, the vertebral, column ; *b*, the œsophagus or gullet ; *c*, the wind-pipe ; *d*, the thyroid cartilage of the larynx ; *e*, the epiglottis ; *f*, the uvula ; *g*, the opening of the left Eustachian tube ; *h*, the opening of the left lachrymal duct ; *i*, the hyoid bone ; *k*, the tongue ; *l*, the hard palate ; *m*, *n*, the base of the skull ; *o*, *p*, *q*, the superior, middle, and inferior turbinal bones. The letters *g*, *f*, *e*, are placed in the pharynx.

end of the pharyngeal bag passes into the gullet or œsophagus (*b*), a muscular tube, which affords a passage into the stomach.

There are no fewer than six distinct openings into the front part of the pharynx—four in pairs, and two single ones in the middle line. The two pairs are, in front, the hinder openings of the nasal cavities; and at the sides, close to these, the apertures of the **Eustachian tubes** (*g*). The two single apertures are, the hinder opening of the mouth between the soft palate and the epiglottis; and, behind the epiglottis, the upper aperture of the respiratory passage, or the **glottis.**

Each of the thirty-two teeth which have been mentioned consists of a **crown** which projects above the gum, and of one or more **fangs**, which are embedded in sockets, or what are called **alveoli**, in the jaws (see Fig. 3).

The eight teeth on opposite sides of the same jaw are constructed upon exactly similar patterns, while the eight teeth which are opposite to one another, and bite against one another above and below, though similar in kind, differ somewhat in the details of their patterns.

The two teeth in each eight which are nearest the middle line in the front of the jaw, have wide but sharp and chisel-like edges. Hence they are called **incisors**, or cutting teeth. The tooth which comes next is a tooth with a more conical and pointed crown. It answers to the great tearing and holding tooth of the dog, and is called the **canine** or eye-tooth. The next two teeth have broader crowns, with two cusps, or points, on each crown, one on the inside and one on the outside, whence they are termed **bicuspid** teeth, and sometimes false grinders. All these teeth have usually one fang each, except the bicuspid, the fangs of which may be more or less completely divided into two. The remaining teeth have two or three fangs each, and their crowns are much broader. As they crush and grind the matters which pass between them they are called **molars**, or true grinders. In the upper jaw their crowns present four points at the four corners, and a diagonal ridge connecting two of them. In the lower jaw the complete pattern is five-pointed,

there being two cusps on the inner side and three on the outer. Each tooth presents a **crown**, which is visible in the cavity of the mouth, where it becomes worn by attrition with the tooth opposite to it and with the food; and one or more **fangs**, which are buried in a socket furnished by the jawbone and the derma of the dense mucous membrane of the mouth, which constitutes the **gum**. The line of junction between the crown and the

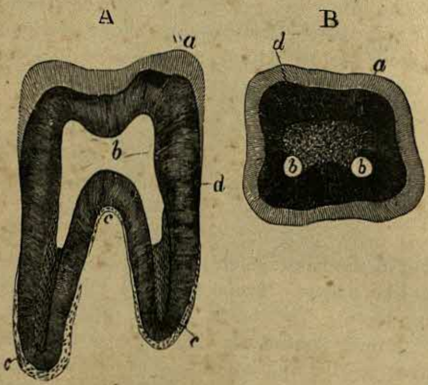

FIG. 70.

A, vertical, B, horizontal section of a tooth.—*a*, enamel of the crown; *b*, pulp cavity; *c*, cement of the fangs; *d*, dentine. (Magnified about three diameters.)

fang is the **neck** of the tooth. In the interior of the tooth is a cavity communicating with the exterior by canals, which traverse the fangs and open at their points. This cavity is the **pulp cavity**. It is occupied and completely filled by a highly vascular tissue richly supplied with nerves, the **dental pulp**, which is continuous below, through the openings of the fangs, with the vascular dermis of the gum which lies between the fangs

and the alveolar walls, and plays the part of periosteum to both.

The tissue which forms the chief constituent of a tooth is termed **dentine** (Fig. 70, A, B, *d*). It is a dense calcified substance containing less animal matter than bone, and further differing from it in possessing no lacunæ, or proper canaliculi. Instead of these it presents innumerable, minute, parallel, wavy tubules (Fig. 71, *d*), which give off lateral branches. The wider inner ends of these tubules may measure 4μ or 9μ ($\frac{1}{5000}$ inch); they open into the pulp cavity, while the narrower outer terminations ramify at the surface of the dentine, and may even extend into the enamel or cement (Fig. 71).

The greater part of the crown and almost the whole of the fangs consist of dentine. But the summit of the crown is invested by a thick layer of a much denser tissue, which contains only 2 per cent. of animal matter, and is the hardest substance in the body; so hard that it will strike fire with steel. This is called **enamel** (Fig. 70, A, B, *a*). It becomes thinner on the sides of the crown and gradually dies out on the neck. Examined microscopically, the enamel is seen to consist of six-sided prismatic fibres (Fig. 71, A, B) set closely side by side, nearly at right angles to the surface of the dentine. These fibres measure not more than 3μ to 5μ ($\frac{1}{8000}$ to $\frac{1}{5000}$ inch) in transverse diameter and present transverse striations.

The third tissue found in teeth is a thin layer of true bone, generally devoid of Haversian canals, which invests the outer surface of the fangs and thins out on the neck. This is termed **cement** (Fig. 70, A, *c*; and Fig. 71, C).

The dental pulp is chiefly composed of delicate connective tissue. It is abundantly supplied with vessels and nerves, which enter it through the small opening at the extremity of the fang. The nerves are mainly sensory branches derived from the fifth pair of cranial nerves.

The superficial part of the pulp, which is everywhere in

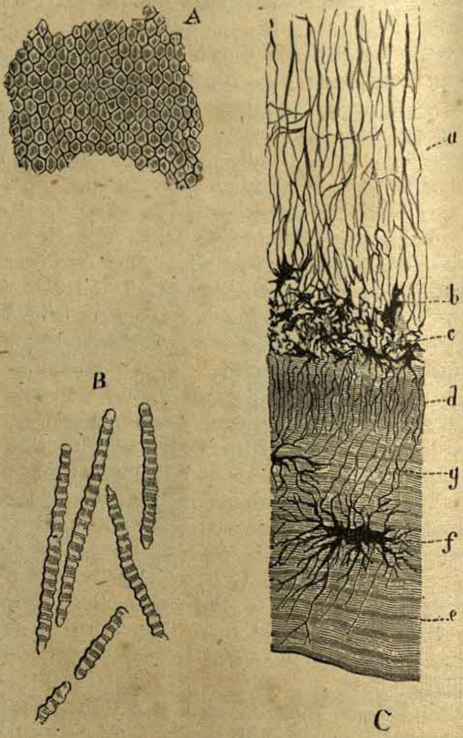

FIG. 71.

A. Enamel fibres viewed in transverse section.
B. Enamel fibres separated and viewed laterally.
C. A section of a tooth at the junction of the dentine (*a*) with the cement (*e*); *b*, *c*, irregular cavities in which the tubules of the dentine end; *d*, fine tubules continued from them; *f*, *g*, lacunæ and canaliculi of the cement. (Magnified about 400 diameters.)

immediate contact with the inner surface of the dentine, consists of a layer of nucleated cells so close set that they

almost resemble an epithelium. They are, however, in reality connective-tissue cells, and the layer is merely a slightly modified condition of the stratum of undifferentiated connective tissue, which lies at the surface of every dermic structure, and from them long filamentous processes can be traced into the dentinal tubules.

The muscles of the parts which have been described have such a disposition that the lower jaw can be depressed, so as to open the mouth and separate the teeth; or raised, in such a manner as to bring the teeth together; or more obliquely from side to side, so as to cause the face of the grinding teeth and the edges of the cutting teeth to slide over one another. And the muscles which perform the elevating and sliding movements are of great strength, and confer a corresponding force upon the grinding and cutting actions of the teeth.

When solid food is taken into the mouth, it is cut and ground by the teeth, the fragments which ooze out upon the outer side of their crowns being pushed beneath them again by the muscular contractions of the cheeks and lips; while those which escape on the inner side are thrust back by the tongue, until the whole is thoroughly rubbed down.

While mastication is proceeding, the salivary glands pour out their secretion in great abundance, and the saliva mixed with the food, which thus becomes interpenetrated not only with the salivary fluid, but with the air which is entangled in the bubbles of the saliva.

When the food is sufficiently ground it is collected, enveloped in saliva, into a mass or bolus, which rests upon the back of the tongue, and is carried backwards to the aperture which leads into the pharynx. Through this it is thrust, the soft palate being lifted and its pillars being brought together, while the backward movement of the tongue at once propels the mass and causes the epiglottis to incline backwards and downwards over the glottis,

and so to form a bridge by which the bolus can travel over the opening of the air-passage without any risk of tumbling into it. While the epiglottis directs the course of the mass of food below, and prevents it from passing into the trachea, the soft palate guides it above, keeps it out of the nasal chamber, and directs it downwards and backwards towards the lower part of the muscular pharyngeal funnel. By this the bolus is immediately seized and tightly held, and the muscular fibres contracting above it, while they are comparatively lax below, it is rapidly thrust into the œsophagus.

The œsophagus is lined with mucous membrane. This rests on some fibrous tissue, outside of which is a thick coat of muscular tissue, striated in the upper third of the tube, unstriated lower down next to the stomach. This is arranged in two layers, an outer layer in which the fibres run parallel to the long axis of the tube; an inner layer in which the fibres are wrapped round the tube.

When food has been thrust into the œsophagus by the action of the pharynx, the muscular wall of the œsophagus just above the bolus contracts and pushes it down into the next lower part. Then the wall of this part contracts and pushes the mass a little further down and so on. In this way the food is finally thrust into the stomach by a series of contractions of each part of the œsophagus in succession: this is spoken of as **peristaltic action.**

Drink is taken in exactly the same way as food. It does not fall down the pharynx and gullet, but each gulp is grasped and passed down. Hence it is that jugglers are able to drink standing upon their heads, and that a horse, or ox, drinks with its throat lower than its stomach, feats which would be impossible if fluid simply fell down the gullet into the gastric cavity.

During these processes of mastication, insalivation, and deglutition, what happens to the food is, first, that it is reduced to a coarser or finer pulp: secondly, that any

matters it carries in solution are still more diluted by the water of the saliva; thirdly, that any starch it may contain begins to be changed into sugar by the saliva, whose formation and action we must next consider.

5. **The Salivary Glands.**—The mucous membrane which lines the mouth and the pharynx is beset with minute glands, the *buccal glands*; but the great glands from which the cavity of the mouth receives its chief

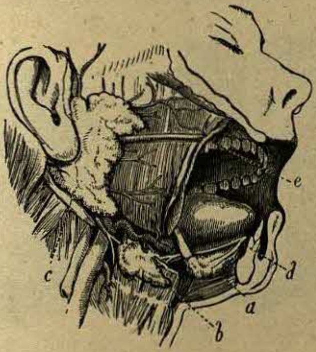

FIG. 72.

A dissection of the right side of the face, showing, *a*, the sublingual, *b*, the submaxillary glands, with their ducts opening beside the tongue in the floor of the mouth at *d*; *c*, the parotid gland and its duct, which opens on the side of the cheek at *e*.

secretion are the three pairs which, as has been already mentioned, are called **parotid, submaxillary, sub-lingual**, and which secrete the principal part of the saliva (Fig. 72).

Each parotid gland is placed just in front of the ear, and its duct passes forwards along the cheek, until it opens in the interior of the mouth, opposite the second upper grinding tooth.

The submaxillary and sublingual glands lie between the lower jaw and the floor of the mouth, the submaxillary being situated further back than the sublingual. Their ducts open in the floor of the mouth below the tip of the tongue. The secretion of these salivary glands, mixed with that of the small glands of the mouth, constitutes the **saliva**.

The salivary glands are built up on the type shown in Fig. 68, 6. The essential part of the structure lies in the

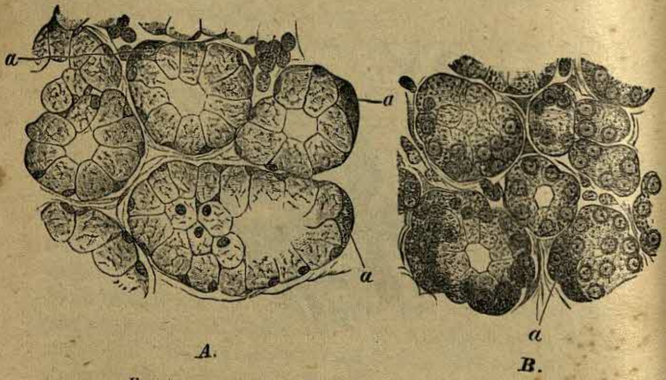

FIG. 73.—SECTIONS OF THE SUBMAXILLARY GLAND.
A, at rest; B, after secretory activity.
a, *a*, demilune cells.

cells which line the dilated ends, or **alveoli**, of the finest branches of their ducts. In a section of a submaxillary gland which is *resting*, that is, *has not been secreting for some time*, the cells are large and nearly fill the alveoli. Each cell has a nucleus placed near its outer end and surrounded by a small amount of protoplasm which is granular and stains readily. The (larger) rest of the cell is quite clear and transparent and stains with great difficulty if at all (Fig. 73, A). Since the material compos-

ing this clear part of the cell is of the nature of mucin, the submaxillary gland is spoken of as a **mucous gland.**

In some of the alveoli a second kind of cell may be seen (Fig. 73, A and B, *a*); these lie close against the outer wall of the alveolus, and from their shape are often called **demilune** cells. They are granular and stain deeply.

In similar sections of the parotid gland, also *in the resting condition*, the cells are smaller than in the alveoli of the submaxillary gland. Further, the nucleus lies near

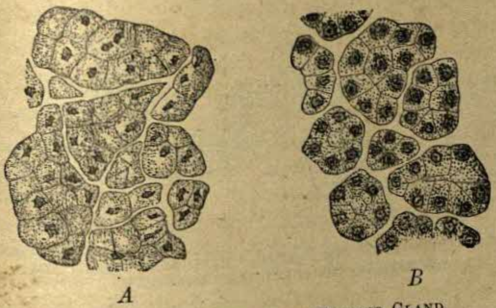

FIG. 74.—SECTIONS OF THE PAROTID GLAND.

A, at rest; B, after secretory activity.

the middle of each cell, and the whole cell is extremely granular and stains fairly easily (Fig. 74, A). The body of each cell is composed of albumin and is free from any trace of anything like mucin; hence the parotid is known as an **albuminous gland.**

After these glands have been *secreting for hours*, as the result of stimulating the nerves supplied to them, the appearance of their cells is greatly changed. The cells of the submaxillary gland are now *smaller*; the nucleus is nearer the centre of each cell and the whole

increased secretion takes place. No clearer proof could be desired to show that when the gland secretes it is because *the impulses which reach it along the nerve exert a direct influence on its cells.* These impulses make the cells take up water and discharge it, together with some of their stored up cell-substance, as saliva which passes as the secretion of the gland into the ducts. It is thus not the increased blood-supply which causes the secretion, although of course it is necessary if the cells are to continue to secrete, for it is from the blood alone that they can obtain all that they require for the manufacture of their secretion.

Saliva is ordinarily secreted in increased quantity as soon as food is introduced into the mouth or even smelt. This result is brought about reflexly. The food stimulates the ends of certain nerves (Vth and IXth cranial, see Lesson XI.), which supply the inside of the walls of the mouth or the Olfactory nerve which supplies the nose. Impulses pass up these nerves to the brain, and from this other impulses pass out down to the submaxillary gland and make its cells secrete.

7. The Composition and Action of Saliva.—The mixed saliva from the several glands consists chiefly of water, holding in solution a small amount of proteid matter, some inorganic salts to which its faintly alkaline reaction is due, a small amount of mucin, which gives to saliva its well-known sliminess, and a small quantity of a peculiar substance called **ptyalin**, which has certain very remarkable properties. It does not act on proteids or fats, but if a little saliva, *i.e.* ptyalin, be mixed with ordinary starch-paste and warmed to the temperature of the body, it turns that starch into a sugar identical with that obtained from malt in brewing and hence known as **maltose**.

But although this chemical change is without doubt of some use to the body, its importance must not be overestimated. For in many animals the action of their saliva on starch is very slight, and moreover (see p. 264) the larger

part of the starch we eat is digested, that is changed into a sugar, while the food is in the intestine and under the action of the pancreatic juice. The chief use of the saliva is mechanical rather than chemical, inasmuch as it moistens the food and thereby assists mastication and makes deglutition, or the swallowing of food, easy.

8. Soluble Ferments or Enzymes.—The peculiar substance, ptyalin, to which the chemical action of saliva on starch is due, belongs to a class of substances known as soluble ferments or enzymes. The word ferment was originally applied to a living organism such as yeast which, as in the case of brewing, while converting the sugar in the wort into alcohol causes at the same time, on account of the simultaneous production of carbonic acid gas, a boiling up or frothing of the liquor; hence the name ferment (*fervere*=to boil up).

But it is known now that such organised ferments can be made to yield extracts which may be filtered so as to be quite free from organisms and still be able to produce the same changes as did the cells from which they are prepared. Hence the name of soluble ferment or enzyme (ζυμη=yeast) was given to the substance in solution which can bring about the same changes as the parent cell.

Very little is known of the chemical nature of enzymes, but they are strongly characterised by certain facts as to the conditions under which their action takes place. Thus: (i) Very minute quantities will effect a change in a mass of the substance on which they are working which is enormously large compared with the minute mass of the enzyme. (ii) Their action depends closely on temperature. At 0° C. (32° F.) they cease to act; as the temperature rises they become increasingly active, and are most active at about 40° C. (104° F.). At higher temperatures they become less active and lose their powers permanently if once heated to 100° C. (212° F.) as by boiling: they are then said to be "killed." (iii) Their action in many cases depends on the reaction, whether acid or alkaline or

neutral, of the solution in which they are at work.[1] (iv) Their action stops in presence of an excess of the special products of their activity, and (v) It has not so far been conclusively proved that the enzymes are themselves used up during the changes which they produce on other substances.

Nearly all the chemical changes which the food undergoes in the alimentary canal are brought about by the action of these soluble ferments or enzymes.

9. The Structure of the Stomach.—The stomach, like the gullet, consists of a tube with muscular walls composed of smooth muscular fibres, and lined by mucous membrane; but it differs from the gullet in several circumstances. In the first place, its cavity is greatly larger, and its left end is produced into an enlargement which, because it is on the heart side of the body, is called the **cardiac dilatation** (Fig. 76, *b*). The opening of the gullet into the stomach, termed the **cardiac aperture**, is consequently nearly in the middle of the whole length of the organ, which presents a long, convex, **greater curvature**, along its front or under edge, and a short, concave, **lesser curvature**, on its back or upper contour. Towards its right extremity the stomach narrows, and, where it passes into the intestine, the muscular fibres are so disposed as to form a sort of sphincter around the aperture of communication. This is called the **pylorus** (Fig. 76, *d*).

The muscular coat of the stomach, consisting of unstriated muscular tissue, is made up of two layers, an outer longitudinal and an inner circular, together with a certain amount of muscle fibres which are continuous with the circular fibres of the œsophagus and which, running **obliquely**, merge into the internal circular layer of the stomach. The mucous membrane which

[1] Thus the pepsin of gastric juice acts best in presence of hydrochloric acid and the trypsin of pancreatic juice in presence of sodium carbonate.

lines the stomach is loosely attached to the muscular coat by a layer of fibrous connective tissue. This is called the submucous coat, and it is in this layer that the nerves, blood-vessels and lymphatics run for the supply of the mucous membrane.

The mucous membrane lining the wall of the stomach contains, or rather is made up of, a multitude of small

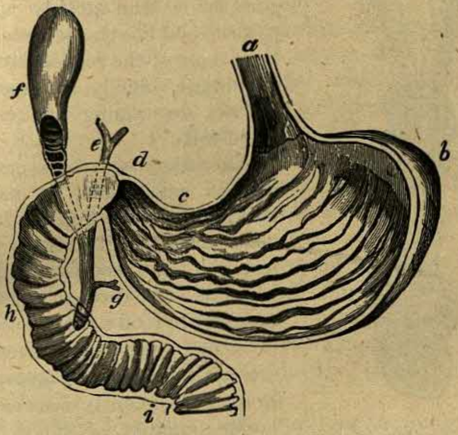

FIG. 76.—THE STOMACH LAID OPEN.

a, the œsophagus; *b*, the cardiac dilatation; *c*, the lesser curvature; *d*, the pylorus; *e*, the biliary duct; *f*, the gall-bladder; *g*, the pancreatic duct, opening in common with the cystic duct opposite *h*; *h*, *i*, the duodenum.

glands, packed closely side by side, which open upon its surface. These are on the whole simple in nature, being long tubular glands, but they vary in character, their blind ends being more divided and twisted at one part of the stomach than another.

Each gland is lined by cells which at the mouth of the gland are columnar and secrete mucin; but deeper down in

the tubes they are cubical and slightly granular. These are the **central cells** (Fig. 77, *c*). A second kind of cell may also be seen lying irregularly scattered between the outer wall of the gland and its central cells: these are the **parietal** or **ovoid cells** (Fig. 77, *p*). Oval in shape, they have a well-defined outline and their cell-substance is usually very distinctly granular. The glands near the pyloric end of the stomach differ from those of the rest of the mucous membrane, chiefly and essentially by not containing any of these ovoid cells.

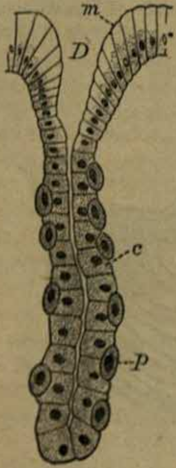

FIG. 77.—ONE OF THE GLANDS WHICH SECRETES GASTRIC JUICE.

D, the duct or mouth of the gland; *m*, mucous cells lining the mouth of the gland and covering the inner surface of the mucous membrane; *c*, central cells; *p*, parietal or ovoid cells.

When the stomach is empty, its mucous membrane is pale and hardly more than moist. Its small arteries are then in a state of constriction, and comparatively little blood is sent through it. On the entrance of food a vaso-motor action is set up, which causes these small arteries to dilate; the mucous membrane consequently receives a much larger quantity of blood, and it becomes very red. At the same time the cells of the gland begin to form their secretion, taking the material they require for this purpose out of the extra supply of blood now coming to them. The whole process is *exactly similar in principle* to that already described in the case of the secretory activity of the submaxillary gland (p. 242).

The secretion thus formed is the **gastric juice.**

10. The Nature and Action of Gastric Juice.—Pure gastric juice is a clear, acid fluid and consists of little more than water, containing a few saline matters in solution, and its acidity is due to the presence of free **hydrochloric acid** to the extent of ·4 per cent. It possesses, however, in addition a small quantity of a peculiar substance called **pepsin**, a soluble ferment or enzyme in many respects similar to, though very different in its effects from ptyalin.

It is easy to ascertain the properties of gastric juice experimentally, by putting a small portion of the mucous membrane of a stomach into water made acid by the addition of ·2—·5 per cent. of hydrochloric acid and containing small pieces of meat, hard-boiled egg, or other proteids, and keeping the mixture at a temperature of about 40° C. (104° F.). After a few hours it will be found that the white of egg, if not in too great quantity, has become dissolved: while all that remains of the meat is a pulp, consisting chiefly of the connective tissue and fatty matters which it contained. This is *artificial digestion,* and it has been proved by experiment that precisely the same operation takes place when food undergoes natural digestion within the stomach of a living animal.

It takes a very long time (some days) for the dilute acid alone to dissolve proteid matters, and hence the solvent power of gastric juice must be chiefly attributed to the pepsin; moreover gastric juice which has been boiled, in which case all the ferment it contains is "killed" (see p. 243), is quite inactive although it contains the usual amount of acid.

Thus gastric juice dissolves proteins, and the characteristic protein which is formed during the solvent action of the juice is called **peptone**, and has pretty much the same characters whatever the nature of the protein which has been digested.

Gastric juice turns milk into curds; whether this coagulating power is due to a particular ferment called **rennin** is less certain than it was formerly supposed to be. It is in all probability the first action of the pepsin on the milk-protein. This is the basis of cheese-making, and the "rennet" used for obtaining the curd in this process is really an extract of the mucous membrane of the stomach of a calf.

Peptone differs from most other proteins in its extreme solubility. Many proteins, as fibrin, are naturally insoluble in water, and others, such as white of egg, though apparently soluble, are not completely so, and can be rendered quite solid or coagulated by being simply heated, as when an egg is boiled. A solution of peptone however is perfectly fluid, does not become solid, and is not at all coagulated by boiling.

As far as we know gastric juice has no direct action on fats, unless in a state of very fine division (emulsion, p. 260); however, by breaking up the protein framework in which animal and vegetable fats are imbedded, it sets these free, and so helps their digestion by exposing them to the action of other agents. Gastric juice has no direct action on carbohydrates. Carbohydrate digestion does take place however in the stomach, especially when large quantities of food are swallowed. The food mixed with the alkaline saliva is only penetrated slowly by the acid secreted by the stomach wall. Whilst this is taking place the saliva has the opportunity of converting starch into sugar. At the end of about twenty minutes it is estimated that carbohydrate digestion in the stomach is brought to a standstill by the hydrochloric acid present.

When food is swallowed it accumulates in the cardiac end of the stomach which gradually distends to receive it. The mass is gradually digested over its surface by the gastric juice. A layer of fluid, of the consistency of pea

soup and to which the name *chyme* is given forms between this mass of food and the stomach wall. The object of the movements of the stomach is in part to work this fluid towards the pylorus. Constrictions form round the stomach and each constriction moves towards the pylorus, and ultimately reaches it. After a time the pylorus, which has hitherto been closed, opens on the arrival of one of these waves and some chyme is passed into the intestine.

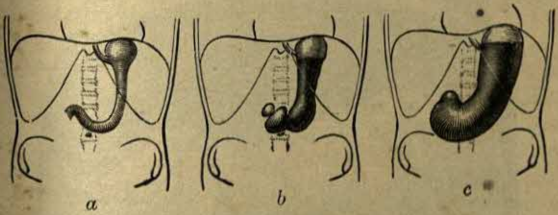

FIG. 78.

a, the stomach, empty; *b*, shortly after a meal, showing peristaltic constrictions; *c*, full.

The pylorus then closes and remains closed till the chyme in the intestine loses its acid reaction and becomes alkaline as we shall see later is the case (p. 263). In this way the larger part of the chyme is allowed to enter the duodenum; but a portion of the fluid (consisting of a little fat together with some sugar may be at once absorbed, making its way, by imbibition, through the walls of the delicate and numerous vessels of the stomach into the current of the blood, which is rushing through the gastric veins to the portal vein.

11. The General Arrangement and Structure of the

FIG. 79.—THE VISCERA OF A RABBIT AS SEEN UPON SIMPLY OPENING THE CAVITIES OF THE THORAX AND ABDOMEN WITHOUT ANY FURTHER DISSECTION.

A, cavity of the thorax, pleural cavity on either side; *B*, diaphragm; *C*, ventricles of the heart; *D*, auricles; *E*, pulmonary artery; *F* aorta;

Intestines.—The intestines form one long tube, with mucous and muscular coats, like the stomach; and, like it, they are enveloped in peritoneum. They are divided into two portions—the **small intestines** and the **large intestines**; the latter, though shorter, having a much greater diameter than the former. The name of **duodenum** is given to that part of the small intestine, about ten inches in length, which immediately succeeds the stomach, and is bent upon itself and fastened by the peritoneum against the back wall of the abdomen, in the loop shown in Fig 76, *h*, *i*. It is in this loop that the head of the pancreas lies (Fig. 67).

The rest of the small intestines, of which the part next to the duodenum is called the **jejunum** and the rest the **ileum**, is no wider than the duodenum, so that the transition from the small intestine to the large (Fig. 80 *Il*) is quite sudden. The opening of the small intestine into the large is provided with prominent lips which project into the cavity of the latter, and oppose the passage of matters from it into the small intestine, while they readily allow of a passage the other way. This is the **ileo-cæcal valve.**

The large intestine forms a blind dilatation beyond the ileo-cæcal valve, which is called the **cæcum**; and from this an elongated, blind process is given off, which, from its shape, is called the **vermiform appendix** of the cæcum (Fig. 80 *verm*).

The cæcum lies in the lower part of the right side of the

G, lungs collapsed, and occupying only back part of chest; *H*, lateral portions of pleural membranes; *I*, cartilage at the end of sternum (ensiform cartilage); *K*, portion of the wall of body left between thorax and abdomen; *a*, cut ends of the ribs; *E*, the liver, in this case lying more to the left than the right of the body; *M*, the stomach, a large part of the greater curvature being shown; *N*, duodenum; *O*, small intestine; *P*, the cæcum, so largely developed in this and other herbivorous animals; *Q*, the large intestine.

abdominal cavity. The **colon**, or first part of the large intestine, passes upwards from it as the **ascending colon**; then making a sudden turn at a right angle, it

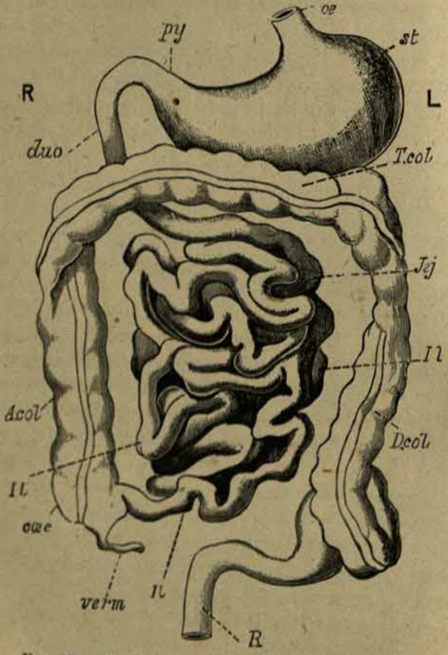

FIG. 80.—THE ALIMENTARY CANAL IN THE ABDOMEN.

R, right; L, left; *œ*, œsophagus; *st.* stomach; *py.* pylorus; *duo.* duodenum; *Jej.* jejunum; *Il.* ileum; *cæc.* cæcum; *A.col.* ascending colon; *T.col.* transverse colon; *D.col.* descending colon; *R*, rectum; *verm.* vermiform appendix.

passes across to the left side of the body, being called the **transverse colon** in this part of its course; and next

suddenly bending backwards along the left side of the abdomen, it becomes the **descending colon.** This reaches the middle line and becomes the **rectum,** which is that part of the large intestine which opens externally.

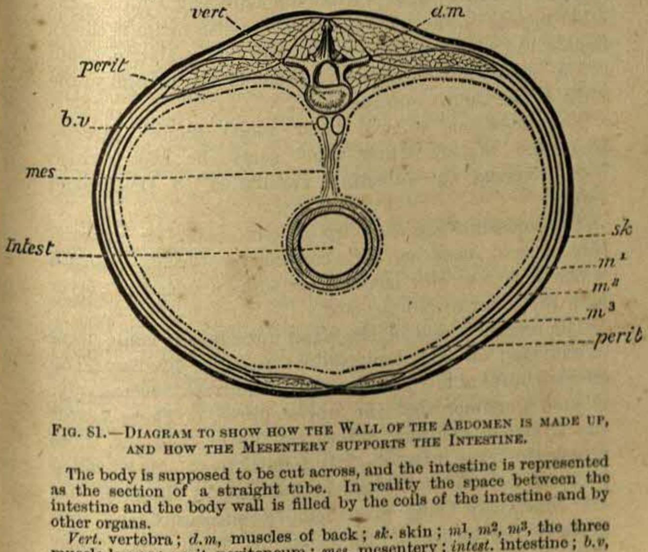

FIG. 81.—DIAGRAM TO SHOW HOW THE WALL OF THE ABDOMEN IS MADE UP, AND HOW THE MESENTERY SUPPORTS THE INTESTINE.

The body is supposed to be cut across, and the intestine is represented as the section of a straight tube. In reality the space between the intestine and the body wall is filled by the coils of the intestine and by other organs.

Vert. vertebra; *d.m,* muscles of back; *sk.* skin; m^1, m^2, m^3, the three muscle layers; *perit.* peritoneum; *mes.* mesentery; *intest.* intestine; *b.v,* blood-vessels.

The intestines are slung from the middle line, along the vertebral column, of the abdominal cavity by a thin membrane known as the **mesentery.** This consists really of two layers between which the nerves, blood-vessels and lymphatics lie which supply the intestines. These layers are continued outwards on each side from

the middle line as a lining, the **peritoneum**, for the whole cavity of the abdomen, and also pass over and round the intestines. The latter thus lie in a fold of the peritoneum, somewhat as a man lies when slung in a hammock (Fig. 81).

Other folds of the peritoneum similarly support the other organs in the abdomen. The peritoneum is thus a double bag whose relation to the wall of the abdomen and to the organs in it is similar to that of the pleuræ to the walls of the thorax and the lungs.

The intestines receive their blood almost directly from the aorta. Their veins carry the blood which has traversed the intestinal capillaries to the portal vein.

The intestines are made up of four coats: an external thin *serous* covering of connective tissue, beneath which is a *muscular* coat connected by a *submucous* layer with the inner or *mucous* coat.

The muscular coat of the small intestines is made up of two layers; an outer longitudinal, an inner circular. The circular fibres of any part are able to contract, successively, in such a manner that the upper fibres, or those nearer the stomach, contract before the lower ones, or those nearer the large intestine. It follows from this so-called *peristaltic contraction*, that the contents of the intestines are constantly being propelled, by successive and progressive narrowing of their calibre, from their upper towards their lower parts. And the same peristaltic movement goes on in the large intestine from the ileocæcal valve to the anus.

The submucous layer is composed of loose (areolar) connective tissue, and carries the blood-vessels, nerves, and lymphatics.

The tube of mucous membrane which forms the inner coat of the small intestines is larger than the muscular tube which surrounds it; hence to get this greater length of the former stowed away into the shorter length of

muscular tubing the mucous membrane is thrown into folds which must evidently lie at right angles to its long axis. These folds serve to increase the surface of the mucous membrane and are called **valvulæ conniventes.**

The large intestine presents noteworthy peculiarities in the arrangement of the longitudinal muscular fibres of the colon into three bands, which are shorter than the walls of the intestine itself, so that the latter is thrown into puckers and pouches (Fig. 79, Q); these are known as the **sacculi,** and serve for the same purpose as the *valvulæ conniventes* of the small intestine. Moreover, the muscular fibres around the termination of the rectum are arranged so as to form a ring-like sphincter muscle, which keeps the aperture firmly closed, except when defæcation takes place.

The mucous membrane of both small and large intestine consists mainly of a number of simple tubular glands packed side by side; they are known as the **glands of Lieberkühn** (Fig. 82, G.L). In the small intestine the tissue between the mouths of the neighbouring glands is at frequent intervals thrown out into the cavity of the intestine as club-shaped processes or projections, the **villi,** which are thus set side by side over the surface of the mucous membrane like the pile on velvet. These villi are absent in the large intestine. The glands of Lieberkühn are separated from each other by tissue which is practically the same as that already described as lymphoid or adenoid tissue (p. 90); it is therefore a network of connective tissue fibres. Wherever a villus occurs this adenoid tissue is prolonged up into and forms the body of the villus, and in it run the finer branches of the blood-vessels and lymphatics supplied to each villus. Each gland of Lieberkühn is lined by a layer of cubical cells, among which occur a certain number of mucous cells, and this layer is continued outwards over each villus as its external covering; but the cells

covering the villi differ in shape from those lining the glands (Fig. 82, B, C).

At irregular intervals along the mucous membrane the lymphoid tissue between the glands is developed into small rounded masses called "**solitary glands**" or "**solitary follicles.**" These closely resemble the glandular substance of the alveoli at the cortex of a lymphatic gland (p. 90), and are similarly crowded with leucocytes. In parts of the small intestine, more particularly in the ileum, groups of these follicles are found packed closely together; they are then known as "agminated glands," or **Peyer's patches**; these do not occur in the large intestine.

At the commencement of the duodenum are certain small racemose glands, called the glands of Brunner, whose ducts open into the intestine. Their function seems to be quite unimportant.

12. **The Structure of the Villi.**—A villus, as already explained, is a projection into the cavity of the intestine of the tissue between the glands of Lieberkühn, and is covered by an epithelium continuous with that which lines these glands. The average length of a villus is about ·5—·7 of a millimetre ($\frac{1}{50}$ - $\frac{1}{36}$ of an inch). Running up the centre or axis of the villus is a relatively large lymphatic vessel which ends blindly at the summit of the villus, but at its base opens into the lymphatics in the submucous tissue (Fig. 82, *l*). This central lymphatic is called a **lacteal.** Lying around the lacteal and parallel to it, are a few small fibres of unstriated muscle derived from the **muscularis mucosæ**, which is a thin layer of unstriated muscle in the mucous membrane, lying next to the submucous coat (Fig. 82, *m.m*); outside these again, close under the epithelium of the villus, is a network of capillaries (Fig. 82, *c*), which receive blood from an artery in the submucous layer and return it by a small vein to the veins of the same layer.

All the space left in between the several structures so

FIG. 82.—DIAGRAM OF TWO VILLI AND AN ADJACENT GLAND OF LIEBERKÜHN (HARDY).

A, two villi with a gland of Lieberkühn, G.L, between their bases; *m.m*, muscularis mucosæ; *l*, central lacteal; *c*, blood-capillaries.

B, portion of epithelium of villus more highly magnified to show one "goblet" cell (above) and two of the other epithelial cells; C, two of the cells which line the tube of the gland of Lieberkühn, more highly magnified.

far described in the body of the villus is filled up with adenoid (lymphoid) tissue, whose meshes are more or less crowded with leucocytes.

The epithelium covering a villus is made up of cells of two kinds. Of these the large majority are tall, columnar, and granular, with an oval nucleus towards their inner end. The outer end of each cell (on the surface of the villus) shows a narrow, strongly striated border (Fig. 82). Lying between these are cells which, from their shape, are often called "goblet" cells, but which in structure are practically the same as the mucous cells of the submaxillary gland already described (p. 238). These cells secrete the mucus which covers the inside of the intestine. The columnar cells are concerned in the absorption of digested food.

13. The Structure of the Pancreas and its Changes during Secretion.—The pancreas is a racemose gland, but the alveoli in which the ducts end are somewhat elongated as compared with their more rounded shape in the salivary glands. The cells in each alveolus are not unlike those of the parotid gland (p. 239). When the gland has been at rest for some time the cells are large, their outlines indistinct, and the central part of each is thickly loaded with very obvious granules (Fig. 83, A). After the gland has been secreting for some time, the cells are smaller, their outline distinct, and the granules have largely disappeared. Those granules which remain are now placed at the inner ends of the cells next to the lumen of the alveolus (Fig. 83, B). These differences in the appearance of the cells in the two conditions of rest and activity show quite clearly that while at rest these cells build up material which is lodged in their substance as obvious granules and discharge this material as part of the secretion as soon as they become active. Thus the changes taking place in the cells of the pancreas during secretion are essentially the same as those previously described in the case of the salivary glands, and have

the same significance in explanation of the phenomena of secretion. In one respect there is a remarkable difference between the pancreas and the salivary glands. The latter always secrete as the result of a stimulus reaching them along their nerves. It is not certain that the cells of the pancreas are supplied with nerves at all and it is certain that they can be made to secrete by a chemical substance which is carried to them by the blood. This hormone (p. 26) is called **secretin** and is manu-

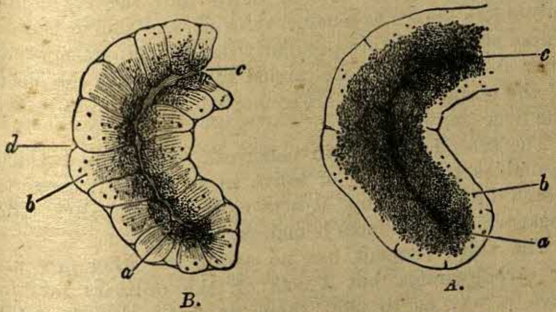

FIG. 83.—A PORTION OF THE PANCREAS OF A RABBIT.

A, at rest; B, in a state of activity.
a, granular central zone of the cells; *b*, clear outer zone; *c*, lumen of alveolus; *d*, junction of two neighbouring cells.

factured in the cells of the mucous membrane of the duodenum. The arrival of acid food from the stomach into the duodenum causes the secretin to be discharged into the blood by which it is carried to the pancreas. By this mechanism a flow of pancreatic juice is insured for the digestion of the food which arrives in the duodenum.

14. The Nature and Action of Pancreatic Juice.—Pancreatic juice is a somewhat viscid fluid, alkaline from the presence of sodium carbonate and containing a fairly large amount of protein in solution. It contains further, as its most important constituents, three soluble ferments.

Of these the chief is one which is called **trypsin**, and is so far like pepsin that it converts proteins into peptones,[1] but it differs from pepsin in several respects. In the first place trypsin is most active in an alkaline solution, such as of 1 per cent. sodium carbonate, while pepsin will only act in presence of an acid. In the next place, the change which proteins undergo by the action of trypsin does not end with the formation of peptones, as it does in the case of pepsin, but proceeds further, and some of the peptone is broken down into the crystalline substances known as leucine, tyrosine, and similar bodies. These amino-acids are peculiarly interesting, inasmuch as after absorption they are carried to the liver in the blood of the portal vein and are converted in part into urea by the liver (see p. 189).

The second ferment in pancreatic juice is one which resembles the ptyalin of saliva in so far as it converts starch into sugar, but it acts more energetically. The sugar which it produces is maltose ($C_{12}H_{22}O_{11}$).

The third ferment has no action on either proteins or carbohydrates, but it acts on the ordinary fats in such a way as to split them up into glycerine and a fatty acid. The latter uniting with the alkali of the pancreatic juice forms soaps, and this process is known as **saponification**. The soaps so formed are soluble substances and therefore can pass into the wall of the intestine. In this form then the fat can be absorbed. Moreover, they help greatly in reducing the remaining fats to that state of fine subdivision, known as an **emulsion**,[2] which, as we shall see presently, is an important preliminary to the digestion of fat in the intestines.

[1] An artificial pancreatic digestion of proteids may be carried on in the way already described for pepsin (p. 247), using as a digestive fluid a 1 per cent. solution of sodium carbonate to which some of the extract of pancreas sold as "liquor pancreaticus" has been added.

[2] When a substance is sub-divided into extremely minute particles suspended in a fluid under conditions such that these particles do not run together on standing, the substance is said to be emulsified and the fluid is called an emulsion. Thus milk is a typical emulsion.

Pancreatic juice, as containing these three ferments. acts therefore on all three classes of foodstuffs, splitting the proteins, saponifying and emulsifying the fats, and converting starch into sugar.

Although the most obvious function of the pancreas is to secrete a digestive juice, there are reasons for supposing that it has other important uses. If it be removed from an animal, a large quantity of sugar (dextrose) speedily appears in the urine and the animal wastes away. Such a condition is not infrequently observed in man, and is known as **diabetes**; and in some cases of diabetes the pancreas has been found to be diseased. In this respect the pancreas seems to exert some control over the nutrition of the body in a way somewhat similar (though differing in its results) to the influence exerted by the thyroid gland and the suprarenal bodies (see pp. 217 and 219). This property of the pancreas is associated with certain groups of cells known as the **Islets of Langerhans** which differ in appearance from the rest of the pancreas.

15. The Nature and Action of Bile.—Bile is the fluid secreted by the liver (see p. 213). In the condition in which it may most ordinarily be observed it has a greenish colour, but as it flows fresh from the liver it is bright yellow with a brownish tinge. This colour is due to a pigment called **bilirubin**. By oxidation this may be easily converted into a green pigment called **biliverdin**, and the differences in the colour of the bile of different animals depends on the relative amounts of these two pigments which they contain. These colouring matters are usually known as the **bile-pigments**, and of these the bilirubin is probably, as already stated (p. 105), formed from the hæmoglobin of the red blood-corpuscles by some peculiar action of the cells of the liver. In addition to the pigments bile, which consists of about 85 per cent. of water, holds in solution certain salts of sodium, the **bile-salts**. These are salts

of two organic acids, one called **glycocholic**, the other **taurocholic**. The former consists of carbon, oxygen, hydrogen, and nitrogen, while the latter contains additionally a considerable quantity of sulphur.

Bile as it is secreted by the liver is a thin fluid, but after its sojourn in the gall-bladder, where it is stored in the intervals between its discharge into the intestines, it contains a considerable amount of **mucin**, secreted into it by the cells which line the gall-bladder and is now viscid and slimy.

Bile has by itself no direct chemical action on food-stuffs. But it serves to neutralise the acidity of the chyme as it leaves the stomach and thus prepares it for the action of pancreatic juice. Further it plays an important part, when mixed with pancreatic juice, in leading to the emulsification of fats, facilitating their subsequent absorption and enabling the ferments of the pancreatic juice to act more rapidly and effectively. It also possesses the property of keeping the bowels sweet. In its absence undue putrefactive changes take place.

16. The Changes Food Undergoes in the Intestines.—The only secretions, besides those of the proper intestinal glands, which enter the intestine, are those of the liver and the pancreas—the *bile* and the *pancreatic juice.* The ducts of these organs have a common opening in the middle of the bend of the duodenum; and, since the common duct passes obliquely through the coats of the intestine, its walls serve as a kind of valve, obstructing the flow of the contents of the duodenum into the duct, but readily permitting the passage of bile and pancreatic juice into the duodenum (Figs. 67 and 76).

The glands of Lieberkuhn are supposed to form a certain amount of a secretion known as **succus entericus**, or intestinal juice, which they then discharge into the intestine.

After gastric digestion has been going on some time, and the semi-digested food begins to pass on into the

duodenum, the pancreas comes into activity, its blood-vessels dilate, it becomes red and full of blood, its cells secrete rapidly, and a copious flow of pancreatic juice takes place along its duct into the intestine.

The secretion of bile by the liver is much more continuous than that of the pancreas, and is not so markedly increased by the presence of food in the stomach. There is, however, a store of bile laid up in the gall-bladder; and as the acid chyme passes into the duodenum, and flows over the common aperture of the bile and pancreatic ducts, a quantity of bile from this reservoir in the gall-bladder is ejected into the intestine. The bile and pancreatic juice together here mix with the chyme and produce remarkable changes in it.

In the first place, the alkali of these juices neutralises the acid of the chyme; in the second place, both the bile and the pancreatic juice appear to exercise an influence over the fatty matters contained in the chyme, which facilitates the subdivision of these fats into very minute separate particles, and this action is specially well-marked when bile and pancreatic juice are mixed. The fat, as it passes from the stomach, is very imperfectly mixed with the other constituents of the chyme; and the drops of fat or oil (for all the fat of the food is melted by the heat of the stomach) readily run together into larger masses. By the combined action, however, of the bile and pancreatic juice the larger drops of fat which pass into the intestine from the stomach are *emulsified*, that is to say are broken up into exceedingly minute particles, and thoroughly mixed with the rest of the contents; they are brought in fact to very much the same condition as that in which fat (*i.e.* butter) exists in milk. When this emulsifying has taken place the contents of the small intestine no longer appear grey like the chyme in the stomach but white and milky; in fact it and milk are white for the same reason, viz., on account of the multitude of minute suspended fatty particles reflecting a great amount of light.

The contents of the small intestine, thus white and milky, are sometimes called *chyle*; but it is best to reserve this name for the contents of the lacteals, of which we shall have to speak directly.

The emulsification and saponification of the fats are not, however, the only changes going on in the small intestine. The pancreatic juice has an action on starch similar to that of saliva, but much more powerful. During the short stay in the mouth very little starch has had time to be converted into sugar, and in the stomach, as we have seen, the action of the saliva is arrested. In the small intestine, however, the pancreatic juice takes up the work again; and indeed, by far the greater part of the starch which we eat is digested, that is, changed into *maltose*, by the action of this juice. A ferment in the succus entericus converts the maltose ($C_{12}H_{22}O_{11}$) into dextrose ($C_6H_{12}O_6$) in which form the sugar is absorbed.

Nor is this all, for, in addition to the above, the alkaline pancreatic juice has a powerful effect on proteins very similar to that exerted by the acid gastric juice; it converts them into peptones, and the peptones so produced do not differ materially from the peptones resulting from gastric digestion. At the same time a variable amount of leucine, tyrosine, and other *amino-acids* make their appearance as the result of the further action of pancreatic juice on the first-formed peptones. Here again the succus entericus aids digestion. Peptone if absorbed into the blood would act as a deadly poison. A ferment *erepsin* also breaks up the peptone into a number of much simpler bodies known as *amino-acids*. These are complicated organic acids which however contain nitrogen in a form closely related to the nitrogen in ammonia and urea.

Hence it appears that, while by the saliva carbohydrates *only*, and by the gastric juice proteins only, are digested, in the intestine all three kinds of food-stuffs, proteins, fats, and carbohydrates, are completely dis-

solved, and made diffusible and so prepared for their passage into the vessels.

As the food is thrust along the small intestines by the grasping action of the peristaltic contractions, the digested matter which it contains is absorbed, that is, passes away from the interior of the intestine into the blood-vessels and lacteals lying in the intestinal walls.

All the way down the small intestines, the proteins, carbohydrates, and fats of a meal are being dissolved or otherwise changed, and passing away into the lacteals or blood-vessels. So that, by the time the contents of the intestine have reached the ileo-cæcal valve, a great deal of the nutritious matter has been removed. Still, even in the large intestine, some nutritious matter has still to be acted upon; and we find that in the cæcum and commencement of the large intestine, changes are taking place, apparently somewhat of the nature of fermentation, whereby the contents become acid. But these changes do not appear to be brought about by any soluble ferments secreted by the walls of this intestine; on the contrary they are largely the result of the activity of certain minute organisms or organised ferments (bacteria, &c.).

In herbivora a considerable quantity of the cellulose they eat does not reappear in the fæces and a small amount may be digested in man. The digestion of cellulose probably takes place in the large intestine and is brought about by the action of micro-organisms.

One marked feature of the changes undergone in the large intestine is the rapid absorption of water. Whereas in the small intestine, the amount of fluid secreted into the canal about equals that which is removed by absorption, so that the contents at the ileo-cæcal valve are about as fluid as they are in the duodenum; in the large intestine on the contrary, especially in its later portions, the contents become less and less fluid. At the same time a characteristic odour and colour are developed, and

the remains of the food, now consisting either of undigestible material, or of material which has escaped the action of the several digestive juices, or withstood their influence, gradually assume the characters of fæces.

17. Absorption from the Intestines.—A great deal of the absorption takes place in the small intestine (though the process is continued on in the large intestine), and there can be no doubt that it is largely effected by means of the villi. Each villus, as we have seen (p. 257), is covered by a layer of epithelium, and contains in the centre a lacteal radicle, between which and the epithelium lies a network of capillary blood-vessels embedded in a delicate tissue. The soap and fatty acids pass into the cells of the epithelium where they reunite with glycerine to form droplets of fat which travel past the capillary blood-vessels, into the central lacteal radicle; so that, after a fatty meal, these lacteal radicles of the villi become filled with fat. The lacteal radicle is continuous with the interior of the lymphatic vessels which ramify in the walls of the intestine, and which pass into the large lymphatic vessels running along the mesentery towards the thoracic duct. Into these vessels the finely divided fat passes from the lacteal radicle of the villus, and, mixing with the ordinary lymph contained in the vessels, gives their contents a white, milky appearance. Lymph thus white and milky from the admixture of a large quantity of finely divided fat is called chyle; and this white chyle may after a meal be traced along the lymphatics of the mesentery to the thoracic duct, and along the whole course of that vessel to its junction with the venous system. After a meal, in fact, this vessel is continually pouring into the blood a large quantity of chyle, *i.e.* of lymph made white and milky by the admixture of fats drawn from the villi of the small intestine.

In the case of the proteins and carbohydrates, the result of digestion has been to produce a solution of nitrogenous organic acids and sugars which are extremely

soluble and highly diffusible. Now we know that if such a solution is separated by a thin membrane from a solution of ordinary non-diffusible proteins, there would be a rapid transmission of the diffusible substances through and across the membrane. The conditions necessary for such a process are evidently present in the intestines where the solution in its interior is separated by what is practically a thin membrane from the (albuminous) blood in the capillaries just below the epithelial cells. It is thus very tempting to suppose that the absorption of amino-acids and sugars (also of salts) is the result of their diffusibility and of the conditions to which they are exposed. And indeed *within certain limits* this view is correct. But it does not by any means explain the whole process. For if substances of differing diffusibilities be placed in the intestines it is not found that the most diffusible substance is necessarily absorbed the fastest. In fact we find that the details of the absorption are in many ways so peculiar that we must again, as in the case of the fats, look to the *living* epithelial cells of the villi as determining and completely controlling the process, which is thus partly physical but chiefly due to the special activity of cells.

The fats pass, as already stated, into the lacteals and thence through the lymphatic vessels and thoracic duct into the blood. Amino-acids and sugar, on the other hand, appear to be taken up by the capillary blood-vessels of the villus, so that very little if any of them gets to the lacteal radicle. From the capillaries of the villi the amino-acids and sugar are then carried along the *portal vein* to the liver, where they probably undergo some further change. So that while the fat reaches the blood very little changed, the cleavage products of the proteins and the sugars though also taking a roundabout course, viz., by the liver, are probably altered before they are thrown into the general blood-stream; for the portal blood in which they are carried is acted upon by the

liver before it flows through the hepatic vein into the general venous system. But concerning both the process of absorption itself and the changes undergone by the absorbed products before they reach the heart, ready to be distributed all over the body, we have probably much yet to learn.

PART II.—FOOD AND NUTRITION.

1. Some Aspects of Nutrition.—Nutrition, on the statistical side, has also to deal with the quantitative relationships between the amount of food supplied and the amount of waste excreted; to strike a balance between the two and to draw conclusions from the balance-sheet as to how the business of the body is being carried on. Further, since food not only repairs waste but also provides energy, the balance-sheet must take into account how much total energy is supplied in the food and how this available income is expended as heat and work.

2. Some Statistics of Nutrition.—The average weight of a healthy full-grown man may be taken as 70 kilogrammes (154 pounds). Such a body is made up, in round numbers, as follows :—

Muscles and Tendons	42	per cent.
Skeleton	16	,,
Skin	7	,,
Fat	19	,,
Brain	2	,,
Thoracic viscera	2	,,
Abdominal viscera	7	,,
Blood	5	,,
	100	,,

The waste which the body excretes and its distribution among the chief excretory organs is shown in the table on the following page, in which the "water and other matters" represent the total waste.

The "other matter" from the lungs is chiefly carbonic acid, in which the larger part of the carbon is excreted, bringing with it nearly all the oxygen originally taken in by the lungs. From the kidneys it includes urea, which contains nearly the whole of the nitrogen excreted, together with some 25 grammes (nearly 1 oz.) of inorganic salts. From the skin the "other matter" is a small amount of salts and some carbonic acid, and in the fæces it includes some 5 grammes of salts. The total output of salts from the body is thus about 30 grammes (or rather more than 1 oz.).

This daily loss has to be made good by the new food supplied. But in calculating the amount of material necessary to replace the waste, we need only turn our attention to the nitrogen and the carbon, for the water lost represents almost entirely water taken as drink or in the food, although a small amount comes from the oxidation of the hydrogen of the food; the oxygen is derived from the air, and the salts are largely, though not entirely, introduced as salts with the food.

The daily waste of nitrogen and carbon may be taken in round numbers as about 20 grammes (300 grains) of the former and 270 grammes (or about 9½ oz.) of the latter. The nitrogen necessary to make good this loss can only be obtained from proteins.

The necessity of constantly renewing the supply of protein matter arises from the circumstance that whether the body is fed or not, a breaking down of protein material is continually going on, giving rise to a constant nitrogenous waste, which leaves the body in the form of urea. Now, this nitrogenous waste, coming from the breaking down of protein material, can only be met by

	Water	and other Matters which contain	Nitrogen	and Carbon.
Lungs	320 grammes (11 oz. or say ½ pint)	778 grammes (27 oz.)	—	225 grammes (8 oz.)
Kidneys	1,500 grammes (53 oz. or say 2½ pints)	65 grammes (2½ oz.)	17 grammes (255 grains)	10 grammes (150 grains)
Skin	650 grammes (23 oz. or say 1 pint)	45 grammes (1½ oz.)	—	7 grammes (100 grains)
Fæces	130 grammes (4 oz.)	52 grammes (say 2 oz.)	3 grammes (45 grains)	30 grammes (450 grains)
	2,600 grammes (6 lbs. or 4½ pints)	940 grammes (2 lbs.)	20 grammes (¾ oz.)	272 grammes (9½ oz.)

fresh protein material being supplied. If protein matter be not supplied, the body must needs waste, because there is nothing in the food competent to make good the nitrogenous loss.

On the other hand, if protein matter be supplied, there is not the same necessity for any other but the mineral food-stuffs, because protein matter contains carbon and hydrogen in abundance, and hence is competent to make good not only the breaking down which is indicated by the nitrogenous loss, but also that which is indicated by the other great products of waste, carbonic acid and water.

In fact, the final results of the oxidation of protein matters are carbonic acid, water, and urea; and these, as we have seen, are the final shapes of the waste products of the human economy.

Proteins contain in round numbers about 15 per cent. of nitrogen, or a little more, and 53 per cent. of carbon, so that the 20 grammes of nitrogen might be obtained from 130 grammes of protein, which would at the same time introduce about 65 grammes of carbon. But the daily waste of carbon is (about) 270 grammes, thus more than 200 grammes of carbon are still required to balance the excess in the excreta. This additional amount of carbon may be obtained from either fats or carbohydrates, but preferably from a mixture of the two. Now fats contain 80 per cent. of carbon, and carbohydrates contain 40 per cent.; thus the desired amount of extra carbon may be obtained by adding to the 130 grammes of protein, about 50 grammes of fats which contain 40 grammes of carbon and 400 grammes of carbohydrates which contain 160 grammes of carbon. Adding to these 30 grammes of inorganic salts and 2,300 grammes of water the total waste is about balanced thus :—

and 2,300 grammes of water the total waste is about balanced thus :—

				Nitrogen.	Carbon.
Proteins	180 grammes	(4½ oz.)	contain	20 grammes (¾ oz.)	70 grammes (2½ oz.)
Fats	50 ,,	(2 oz.)	,,	——	40 ,, (1½ oz.)
Carbohydrates	400 ,,	(14 oz.)	,,	——	160 ,, (5½ oz.)
Salts	30 ,,	(1 oz.)	,,	——	——
Water...	2,300 ,,	(4 pints)	,,	——	——
	2,910 grammes			20 grammes	270 grammes (9½ oz.)

Foods as previously explained (p. 226) never consist, except perhaps in the case of fats and oils, of one kind of food-stuff only ; each article of food contains at most an excess of some one kind of food-stuff, and no two foods are exactly alike. Hence the selection of such foods as will supply the amount of proteids, fats, and carbohydrates required by the above statement opens up the possibility of an almost indefinite choice. But the composition of the more commonly used articles of food as regards the amounts of the several kinds of food-stuffs they contain, has been very carefully determined, so that we may now proceed to select a meal such as will give us the desired quantities of proteins, fats, and carbohydrates.

Suppose, for instance, that we select lean meat, bread, potatoes, milk, and fat, such as butter or dripping, as our food. We may obtain all that we require from the amounts of each food shown in the table on the following page.

The amounts of the several foods shown in the above table suffice to cover the waste shown in the table on p. 270 and constitute what is ordinarily known as a diet. But the data thus given are to be taken rather as an illustration of how the balance-sheet between food and waste is drawn up, than as an example of exactly what a man ought to eat in the way of food. As already pointed out, foods are many, and vary in the relative amounts of the several food-stuffs they contain, so that it is possible to draw up

Quantity.	Kind of Food.	Contains	Provides: Proteins.	Provides: Fats.	Provides: Carbohydrates.
230 grammes (or $\frac{1}{2}$ lb.)	Very lean meat	25 per cent. proteins	58 grammes	—	—
480 grammes (or say 1 lb.)	Bread	8 per cent. proteins; 50 per cent. carbohydrates	39 ,,	—	240 grammes
660 grammes (or say $1\frac{1}{2}$ lb.)	Potatoes	2 per cent. proteins; 21 per cent. carbohydrates	13 ,,	—	140 ,,
500 grammes (or say $\frac{8}{4}$ pint)	Milk	4 per cent. proteins; 4 per cent. fats; 4 per cent. carbohydrates	20 ,,	20 grammes	20 ,,
30 grammes (or say 1 oz.)	Fats.	100 per cent. fats	—	30 ,,	—
2,300 grammes (or say 4 pints)	Water	—	—	—	—
			130 grammes	50 grammes	400 grammes

food-stuffs they contain, so that it is possible to draw up many such tables all satisfying the condition of covering the daily loss of 20 grammes of nitrogen and about 270 or 300 grammes of carbon.

In drawing up such a table of diet the question of cost must also not be forgotten, as in the case of fixing the diet for soldiers or prisoners. Thus, for instance, it costs more to obtain the requisite amount of carbon from fat than from sugar or starch. Moreover, the value of a diet depends also on the ease with which its constituents can be digested and utilised. Mere chemical analysis is by itself a very insufficient guide as to the usefulness and nutritive value of an article of food. A substance to be nutritious must not only contain some or other of the various food-stuffs, but contain them in an available, that is a digestible, form. A piece of beef-steak is far more nourishing than a quantity of pease pudding containing even a larger proportion of proteid material, because the former is far more digestible than the latter; and a small piece of dry hard cheese, though of high nutritive value as judged by mere chemical analysis, will not satisfy the more subtle criticism of the stomach.

3. **The Economy of a Mixed Diet.**—The body, as we have repeatedly pointed out, cannot obtain the nitrogen it requires from any source other than the ready-made proteids. Hence in the absence of these from the food of an animal it must sooner or later die from what is known as **nitrogen starvation.**

In this case, and still more in that of an animal deprived of vital food altogether, the organism, so long as it continues to live, feeds upon itself. In the former case, all the processes involving a loss of nitrogen, in the latter, all the processes leading to the appearance of all the several waste products, are necessarily carried on at the expense of its own body; whence it has been rightly enough observed that a starving sheep is as much a carnivore as a lion. *Protein is thus the essential element of*

all food, and since it contains carbon as well as nitrogen it may suffice, under certain circumstances, to maintain the body; but it is a very disadvantageous and uneconomical food-stuff when taken by itself.

Albumin, which may be taken as a type of the proteins, contains about 53 parts of carbon and 15 of nitrogen in 100 parts. If a man were to be fed on white of egg, therefore, he would take in, speaking roughly, 3½ parts of carbon for every part of nitrogen.

But we have seen that a healthy, full-grown man, keeping up his weight and heat, and taking a fair amount of exercise, eliminates per diem 270 to 300 grammes of carbon to only 20 grammes of nitrogen, or, roughly, only needs one-thirteenth to one-fifteenth as much nitrogen as carbon. However, if he is to get his 270 grammes of carbon out of albumin, he must eat 500 grammes of that substance. But 500 grammes of albumin contain 75 grammes of nitrogen, or nearly four times as much as he wants.

To put the case in another way, it takes about four pounds (1,800 grammes) of fatless meat (which generally contains about one-fourth its weight of dry solid proteins) to yield the necessary amount of carbon, whereas one pound (453 grammes) will furnish all the nitrogen that is required.

Thus a man confined to a purely protein diet must eat an excessive quantity of it in order to obtain the amount of carbon he requires. This not only involves a great amount of physiological labour in comminuting the food, and a great expenditure of power and time in dissolving and absorbing it, but throws a great quantity of wholly profitless labour upon those excretory organs, which have to get rid of the nitrogenous matter, three-fourths of which, as we have seen, is superfluous.

Unproductive labour is as much to be avoided in physiological as in political economy; and it is quite possible that an animal fed with perfectly nutritious protein matter

should die of starvation; the loss of power in various operations required for its assimilation overbalancing the gain; or the time occupied in their performance being too great to permit waste to be repaired with sufficient rapidity. The body, under these circumstances, falls into the condition of a merchant who has abundant assets, but who cannot get in his debts in time to meet his creditors.

These considerations lead us to the physiological justification of the universal practice of mankind in adopting a mixed diet, in which proteins are mixed with fats and carbohydrates.

Fats may be taken to contain about 80 per cent. of carbon, and carbohydrates about 40 per cent. Now it has been seen that there is enough nitrogen to supply the waste of that substance per diem, in a healthy man, in 453 grammes (a pound) of fatless meat which also contains 67 grammes (1,000 grains) of carbon, leaving a deficit of 200 grammes (3,000 grains) of carbon; 250 grammes (say half a pound) of fat, or 500 grammes (rather more than a pound) of sugar, will supply this quantity of carbon.

Several apparently simple articles of food constitute a mixed diet in themselves. Thus butcher's meat commonly contains from 30 to 50 per cent. of fat. Bread, on the other hand, contains the protein gluten, and the carbohydrates, starch and sugar, with minute quantities of fat. But from the proportion in which these protein and other constituents exist in these substances, they are neither, taken alone, such physiologically economical foods as they are when combined in the proportion of about 200 to 75, or two pounds of bread to three-quarters of a pound of meat per diem.

There is one largely consumed article of food which is not merely composed of all the various food-stuffs requisite to provide a mixed diet, but contains these substances in the relative amounts most suitable for affording an economical diet as regards the proportion of the nitrogen to the carbon. This food is milk. Milk consists chiefly

of water (86 p. c.) in which proteins, casein and some albumin, are dissolved, as also a carbohydrate, milk-sugar or lactose, and inorganic salts such as chlorides and phosphates of sodium, potassium and calcium. The fat present in milk is emulsified or suspended in the water in the form of extremely minute globules, and the white appearance presented by milk is due to the great amount of light reflected from these minute particles of fat. Milk, however, is deficient in one essential constituent of diet, that of iron. We have seen that iron is an important constituent of hæmoglobin (p. 97). A child is born with sufficient iron in its body to provide for the formation of red blood corpuscles for nine months to a year. After this period it must get iron from its diet. Milk does not furnish this.

4. The Effects of the several Food-stuffs.—When some protein food is given to an animal, such as a dog, which has been previously starved, the larger part of the nitrogen given in the protein is not retained in the body but is excreted almost immediately. This is the nitrogen in what we have termed the "exogenous" urea (p. 189). The nitrogen excreted during the starvation was of course solely of "endogenous" origin. If another larger meal of protein be given the amount of nitrogen excreted is still further increased, less and less being retained in the body. By proceeding in this way it is possible to increase the excretion of nitrogen to such an extent that it ultimately becomes equal to the amount administered in the food: the animal is then said to be in "nitrogenous equilibrium."

The effects of carbohydrates and fats as foods cannot be studied by feeding an animal with these alone, as is possible with proteins. But this difficulty may be got over by administering a small, *fixed* quantity of protein with a *variable* amount of either carbohydrate or fat. In this case it is found that an increase of the carbohydrate in food very soon leads to the laying on of fat; and this corresponds to the everyday experience which is frequently

embodied in the expression "sugar is fattening." At the same time analysis of the liver shows that a large amount of *glycogen is stored up* in it, as previously explained (p. 215).

If fats be given in increasing quantity they also finally lead to a laying on of fat, but by no means so readily as does an increase of carbohydrates. At the same time, no storage of glycogen is observed in the liver. Fats are therefore not as fattening as might at first sight have been expected.

We have already mentioned **gelatin** as a food-stuff which consists of the same four elements as are present in proteins and in somewhat similar proportions. But the nitrogen in gelatin cannot completely replace that of a protein for the repair of nitrogenous waste. An animal fed with gelatin dies ultimately of "nitrogen starvation," though not as soon as it would without this constituent of food. Thus gelatin reduces the waste of the body and, so far, may be a useful article of food.

Although we have laid stress on the necessity of protein in diet, we should point out the possibility supporting nitrogenous equilibrium on a diet which does not actually contain them. In discussing the digestion and absorption of proteins we saw that they were ultimately absorbed as amino-acids. Of these each protein breaks up into a great many of different characters. If we could collect all these acids and mix them in exactly the correct proportions we could no doubt supply the needs of the body. At present this can be accomplished by artificial digestion of protein and the use of the products as a diet. If, however, such a diet fell short by this amino-acid or that, it would become inadequate. In this fact we find the key to the incompetence of gelatin to support life. When it is digested there are lacking in this mixture of acids produced, two important bodies which are yielded by protein.

Some of these bodies necessary are only required in very small quantities. Orientals can live on a diet which

consists almost entirely of rice, but if the rice be devoid of its natural husks they incur the risk of suffering from a condition of mal-nutrition known as beri-beri. The particular all important constituent of the husks has been isolated and estimated though the amount necessary to the body daily is almost inconceivably small.

The **salts** which leave the body are largely the salts which were introduced in the food. It might therefore at first sight appear that they are merely unavoidable constituents of food which are largely passed without change through the body. But this is not the case. In some way or other the salts of food play an essential part in directing the metabolism taking place in the tissues. Thus animals fed with an abundance of food, which has however been freed as far as possible from salts, soon die with symptoms of defective nutrition, accompanied by paralysis and convulsions.

When an animal is deprived of all food whatsoever, it begins to feed on its own tissues. Thus up to the day of its death from starvation there is an output of urea and of carbonic acid, though in amounts less than when food is being taken. The loss of tissue substance thus produced affects the several tissues to different extents; but without entering into details we may simply point out that the master-tissues suffer least, in the obvious effort to prolong life to the utmost. Thus the brain and spinal cord are almost unaltered at death, and the blood and the muscular tissue of the heart also lose but little as compared with the fat and the skeletal muscles on which the body is now chiefly living.

5. The Erroneous Division of Food-stuffs into Heat-producers and Tissue-formers.—Food-stuffs have been divided into *heat-producers* and *tissue-formers*—the carbohydrates and fats constituting the former division, the proteins the latter. But this is a very misleading, and indeed erroneous classification, inasmuch as it implies, on the one hand, that the oxidation of the proteins does not

develop heat; and, on the other, that the carbohydrates and fats in being oxidised, subserve only the production of heat.

Undoubtedly proteins are *tissue-formers*, inasmuch as no tissue can be produced without them; for all the tissues are nitrogenous, some containing a large and others a small quantity of nitrogen, and proteins are the only nitrogenous food stuffs; they alone can supply the nitrogenous elements of the tissues. But there is reason to think that the fats and carbohydrates taken as food may also be directly built up into the tissues.

Moreover if the proteins alone are the tissue-formers then the energy set free during the contracting activity of the pre-eminently nitrogenous muscles ought to come from the metabolism of their proteins. But this is not found to be the case, for even the most violent muscular exercise does not lead immediately to any increased output of nitrogenous waste which is in the least proportionate to the work being done. On the other hand exercise at once, and largely, increases the excretion of carbonic acid to an extent which may be five times as great as during rest; that is to say, the non-nitrogenous part of the tissue seems to be used up more quickly than the nitrogenous part; and the consumption of this particular constituent of the muscular substance may be made good by non-nitrogenous food, by fats or carbohydrates.

On the other hand, proteins must be regarded as heat-producers also. For if oxidation be, as has been suggested, largely confined to the tissues, though in some tissues, as in muscles, the non-nitrogenous part seems to be most rapidly changed, yet the nitrogenous part, supplied by the proteins, is sooner or later oxidised, and in being oxidised must give rise to heat.

As soon as the elements of the food, in fact, get into the tissues, the distinction between the two classes is lost; both form tissues, and both supply heat.

If it is worth while to make a special classification of

the vital food-stuffs at all, it appears desirable to distinguish the *essential* food-stuffs, or proteins, from the *accessory* food-stuffs, or fats and carbohydrates—the former alone being, in the nature of things, necessary to life, while the latter, however important, are not absolutely necessary.

6. The Income and Expenditure of Energy.—It is quite certain that nine-tenths of the dry, solid food which is taken into the body, sooner or later leaves it in the shape of carbonic acid, water, and urea; and it is also certain not only that the compounds which leave the body are more highly oxidised than those which enter it, but that all the oxygen taken into the blood by the lungs is carried away out of the body in the various waste products.

The intermediate stages of this conversion are, however, by no means so clear. It is highly probable that all the food-stuffs which pass from the alimentary canal into the blood, be they derived from proteins, or fats, or carbohydrates, become part and parcel of some tissue or other (muscle, nervous tissue, glandular tissue, and the like), before they are oxidised; that indeed it is as constituent elements of some tissue or other that they suffer oxidation, and that the amount of oxidation going on in the blood is very small.

In the course of its oxidation, the food not only supplies the energy which the body expends in doing work, but also the energy which, as we have seen, the body loses as heat. The oxidation of the food is indeed the ultimate source of the heat of our bodies, all other causes being of little moment. About this there can be no doubt, and it is further probable that the oxidation which thus gives rise to heat is not the oxidation of the elements of the food as they are carried about in the blood, but the oxidation of them in the tissues, more especially the muscles, in the cells of which they may be pictured in close contact with, and available for, the actual needs of the fabric.

The oxidation of the tissues, which are themselves built up out of food, and hence ultimately the oxidation of the food itself, thus provides for the energy expended as muscular work and as heat. Now the amount of mechanical work a man does may be detremined with no great difficulty, whether we calculate it as work done in walking or in turning some machine or in some other effort which results in overcoming a resistance. This work is measured in terms of the resistance overcome, or weight lifted, multiplied by the height through which it is raised. Thus we speak of the work done in lifting one pound through the height of one foot as a foot-pound; or using the metric system and taking a kilogramme (2·2 lbs.) and a metre (39·37 inches) as the units of weight and distance, we call the unit of work a kilogramme-metre, equal to 7·24 foot-pounds. Using the latter unit we may say that a good day's work is about 150,000 kilogramme-metres.

The unit of heat is the amount of heat required to raise the temperature of one pound of water through 1° F. Now, as is seen in all ordinary engines, heat can do work; and it is found that one unit of heat can do 772 foot-pounds of work. This is called the "mechanical equivalent of heat." In the metric system the unit becomes the amount of heat required to raise the temperature of one gramme (15·4 grains) of water through 1° C. This is called a **calorie**, and the mechanical equivalent of heat is now 424 gramme-metres. Using these data we can readily convert heat into its equivalent of work or *vice versâ*.

The measurement of the amount of heat given off by the body is by no means easy, and the sources of error are considerable. But allowing for these a rough determination may be made, and the heat thus measured may be calculated as work by using the mechanical equivalent of heat and the result added to the actual work done as work. The outcome of this calculation shows that of the

total energy expended by the body about one-sixth is put out as work and five-sixths as heat. Finally we find that the average total output of energy as work and heat (calculated as work) may be taken as about 1,000,000 kilogramme-metres.

We may now consider how far this expenditure is met by the income of energy in food. When a substance is completely burnt, *i.e.* oxidised, to water and carbonic acid, a certain amount of heat is produced which can be measured. Thus it is possible to determine how much heat is produced by the complete combustion of one gramme of each of the food-stuffs, proteins, fats and carbohydrates. The result obtained is as follows :—

1 gramme of protein	gives	5,700	calories.
1 ,, ,, fat	,,	9,500	,,
1 ,, ,, carbohydrate	,,	4,000	,,

Now this must also be the amount of heat produced by the same quantity of each of these food-stuffs during their oxidation in the animal body. In the case of the protein some deduction has to be made because the proteins are not completely oxidised ; the nitrogen they contain leaves the body as urea, which is still capable of undergoing further oxidation to water, nitrogen, and carbonic acid. One gramme of protein gives rise to about ⅓ gramme of urea, and the complete combustion of this amount of urea gives rise to 844 calories. Hence, deducting these from the 5,700 gives us about 4,800 calories, which we may take as being the *physiologically available* heat of combustion of one gramme of protein. If now we apply these values to the diet given on p. 272 we find that :—

130 grammes of protein	give	624,000	calories.
50 ,, ,, fats	,,	475,000	,,
400 ,, ,, carbohydrate	,,	1,600,000	,,
		2,699,000	

If now we take the mechanical equivalent of this heat we find it works out as 1,144,376 kilogramme-metres. Hence the energy available by the oxidation in the body of this particular diet is more than sufficient to balance the total amount which we saw was expended.

LESSON VII

MOTION AND LOCOMOTION

1. The Source of Active Power and the Organs of Motion.—In the preceding Lessons the manner in which the incomings of the human body are converted into its outgoings has been explained. It has been seen that new matter, in the form of vital and mineral food, is constantly appropriated by the body, to make up for the loss of old matter, which is as constantly going on in the shape, chiefly, of carbonic acid, urea, and water the formation of this waste being the outcome of oxidation accompanied by a liberation of energy.

The vital foods are derived directly, or indirectly, from the vegetable world: and the products of waste either are such compounds as abound in the mineral world, or immediately decompose into them. Consequently, the human body is the centre of a stream of matter which sets incessantly from the vegetable and mineral worlds into the mineral world again. It may be compared to an eddy in a river, which may retain its shape for an indefinite length of time, though no one particle of the water of the stream remains in it for more than a brief period.

But there is this peculiarity about the human eddy, that a large portion of the particles of matter which flow into it have a much more complex composition than the particles which flow out of it. To speak in what is not altogether a metaphor, the atoms enter the body for the

most part, piled up into large heaps, and tumble down into small heaps before they leave it. The energy which they set free in this tumbling down, is the source of the active powers of the organism.

These active powers are chiefly manifested in the form of motion—movement, that is, either of part of the body, or of the body as a whole, which last is termed *locomotion*.

The organs which produce total or partial movements of the human body are of three kinds: *cells exhibiting amœboid movements*, *cilia*, and *muscles*.

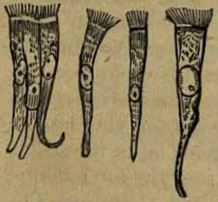

FIG. 84.—COLUMNAR CILIATED EPITHELIUM CELLS FROM THE HUMAN NASAL MEMBRANE.

Magnified 300 diameters. (Sharpey.)

The amœboid movements of the white corpuscles of the blood have been already described, and it is probable that similar movements are performed by many other simple cells of the body in various regions.

The amount of movement to which each cell is thus capable of giving rise may appear perfectly insignificant; nevertheless, there are reasons for thinking that these amœboid movements are of great importance to the economy, and may under certain circumstances be followed by very notable consequences.

2. Ciliated Epithelium and Action of Cilia.—Cilia are filaments of extremely small size, attached by their bases to, and indeed growing out from, the free surfaces of certain epithelial cells; there being in most instances very many (thirty for instance), but, in some cases, only a few cilia on each cell (Figs. 40, 84). In some of the lower animals, cells may be found possessing only a single cilium. They are in incessant waving motion, so long as life persists in them. Their most common form of movement is that each cilium is suddenly bent upon itself,

becomes sickle-shaped instead of straight, and then more slowly straightens again, both movements, however, being extremely rapid and repeated about ten times or more every second. These two movements are of course antagonistic ; the bending drives the water or fluid in which the cilium is placed in one direction, while the straightening drives it back again. Inasmuch, however, as the bending is much more rapid than the straightening, the force expended on the water in the former movement is greater than in the latter. The total effect of the double movement therefore is to drive the fluid in the direction towards which the cilium is bent : that is, of course, if the cell on which the cilia are placed is fixed. If the cell be floating free, the effect is to drive or row the cell backwards ; for the cilia may continue their movements even for some time after the epithelial cell, with which they are connected, is detached from the body. And not only do the movements of the cilia thus go on independently of the rest of the body, but they appear not to be controlled by the action of the nervous system. Each cilium is comparable to one of the mobile processes of a white corpuscle. A ciliated cell differs from an amœboid cell in that its contractile processes are permanent, have a definite shape, and are localised in a particular part of the cell, and that the movements of the processes are performed rhythmically and always in the same way. But the exact manner in which the movement of a cilium is brought about is not as yet thoroughly understood.

Although no other part of the body has any control over the cilia, and though, so far as we know, they have no direct communication with one another, yet their action is directed towards a common end—the cilia, which cover extensive surfaces, all working in such a manner as to sweep whatever lies upon that surface in one and the same direction. Thus, the cilia which are developed upon the epithelial cells, which line the greater part of the nasal cavities and the trachea, with its rami-

fications, tend to drive the mucus in which they work, outwards.

In addition to the air-passages, cilia are found, in the human body, in a few other localities; but the part which they play in man is insignificant in comparison with their function in the lower animals, among many of which they become the chief organs of locomotion.

3. The Structure of Unstriated Muscle.—Unstriated (also called "plain" or "smooth") muscle occurs in the walls of the alimentary canal, the blood-vessels, the bladder, and other organs. It is composed of bands of fibres which are bound together by connective tissue carrying nerves and blood-vessels. The fibres are in reality elongated, flattened, spindle-shaped cells whose

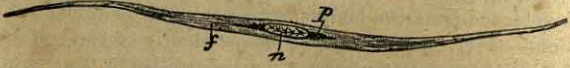

FIG. 85.—A FIBRE-CELL FROM THE PLAIN, NON-STRIATED MUSCULAR COAT OF THE INTESTINE.

f, fibre; *n*, nucleus; *p*, granular protoplasm around the nucleus.

length is about 50μ ($\frac{1}{500}$ inch) and width 6μ ($\frac{1}{4000}$ inch). Somewhere towards the middle of each cell there is an elongated oval or sometimes rod-shaped nucleus, surrounded by a small amount of granular protoplasm which is pointed at the ends of the nucleus.

The substance of the cell is clear and shows no transverse striations, although it often shows signs of a very fine longitudinal fibrillation. A number of such fibre-cells are united together by a minute quantity of cement, or intercellular substance, into a thin flat band, and a number of such bands are bound together by connective tissue into larger bands or bundles. Each fibre is capable of contracting, that is, of shortening and becoming at the same time thicker. In addition to the actual physical

connection which the cement substance affords there is clearly some fundamental connection by which the heat is conducted from fibre to fibre.

4. The Structure of Striated Muscle.—Striated muscle is also made up of fibres, though the fibres are very different from the fibres or fibre-cells of unstriated muscle, and these fibres are again similarly bound up together in various ways, by connective tissue which carries the blood-vessels and nerves, so as to form muscles of various shapes and sizes.[1] Each muscle is thus made up of (i) an external wrapping or **perimysium**; this is a sheath of connective tissue from the inner face of which partitions proceed and divide the space which it incloses into a great number of longitudinally disposed compartments; (ii) the **muscular fibres** which occupy these compartments; (iii) the **vessels** which lie in the sheath and in the partitions between the compartments, and thus surround the muscular fibres without entering them; (iv) the **motor nerves** which also at first lie in the sheath and in the partitions between the compartments, but which eventually enter into the muscular fibres.

The *perimysium* forms a complete envelope around the muscle, which, when it is sufficiently strong to be dissected off, is known as a **fascia**; at each end it usually terminates in dense connective tissue (**tendon**), which becomes continuous with the bone or cartilage to which the tendon is attached. The partitions given off from the inner surface of the perimysium form at first coarse compartments, inclosing large bundles, each consisting of a very great number of fibres. These large bundles are again divided by somewhat finer connective tissue partitions into smaller bundles, and these again into still smaller ones, and so on, the smallest bundles of

[1] It is necessary to distinguish "muscle" as an organ from "muscle" as a tissue. The biceps muscle (p. 306), for example, is an organ of a complicated character, of which muscular tissue forms only the chief constituent.

all being composed of a number of individual muscular fibres (Fig. 86). In this way the partitions become thinner and more delicate, until those which separate the chambers in which the individual muscular fibres are contained are reduced to little more than as much connective tissue as will hold the small nerves, arteries and veins and capillary networks together. As the perimysium consists of connective tissue, it may be destroyed by prolonged boiling in water. In fact, in "meat boiled to rags" we have muscles which have been

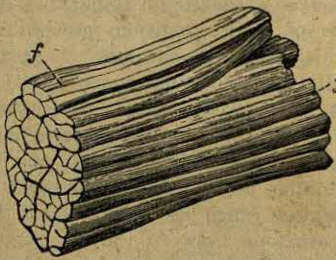

FIG. 86.—FASCICULI OF STRIATED MUSCLE CUT ACROSS.
Several fasciculi *f*, bound together into larger fasciculi to make up the muscle.

thus treated: the perimysial case is broken up, and the muscular fibres, but little attacked by boiling water, are readily separated from one another.

If a piece of muscle of a rabbit which has been thus boiled for many hours, is placed in a watch-glass with a little water, the muscular fibres may be easily teased out with needles and isolated. Such a fibre will be found to have a thickness of somewhere about 60μ ($\frac{1}{400}$ inch) (they vary, however, a great deal), with a length of 30 or 40 millimetres, *i.e.*, about $1\frac{1}{2}$ inch. It is a cylindroidal or polygonal solid rod, which either tapers or is bevelled off

at each end. By these it adheres to those on each side of it; or, if it lies at the end of a series, to the tendon.

The structure and properties of striated muscular tissue in the histological sense means the structure and properties of these fibres.

As we have already had occasion to remark, all tissues undergo considerable alteration in passing from the living

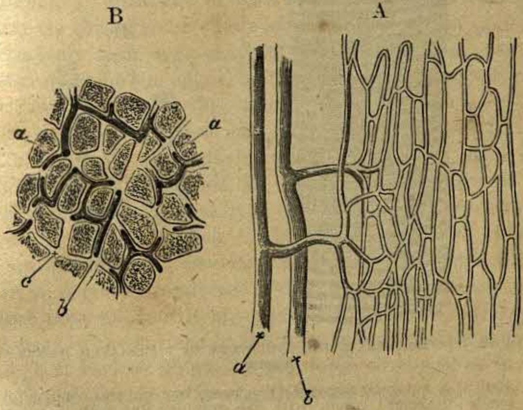

FIG. 87.—CAPILLARIES OF STRIATED MUSCLE.

A. Seen longitudinally. The width of the meshes corresponds to that of an ultimate fibre. *a*, small artery; *b*, small vein.
B. Transverse section of striated muscle. *a*, the cut ends of the ultimate fibres; *b*, capillaries filled with injection material; *c*, parts where the capillaries are absent or not filled.

to the dead state, but, in the case of muscle, the changes which the tissue undergoes in dying, are of such a marked character that the structure of the dead tissue gives a false notion of that of the living tissue.

A living striated muscular fibre of a frog or a mammal is a pale transparent rod composed of a soft, flexible, elastic substance, the lateral contours of which, when the

fibre is viewed out of the body, appear sharply defined, like those of a glass rod of the same size; but when the fibre is observed in the living body, bathed in the lymph which surrounds it, the outlines are not so sharply de-

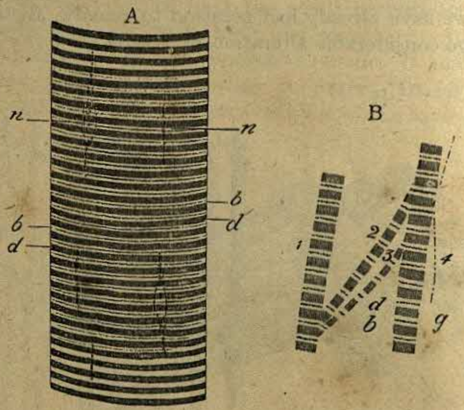

FIG. 88.—TO ILLUSTRATE THE STRUCTURE OF A STRIATED MUSCULAR FIBRE.

A. Part of a muscular fibre (of a frog) seen in a natural condition. *d*, dim bands; *b*, bright bands, with the granular line seen in many of them; *n*, nuclei and the granular protoplasm belonging to them, very dimly seen.

B. Portion of prepared mammalian muscular fibre teased out, showing longitudinal portions of variable (1, 2, 3, 4) thickness; 4 represents the finest portion (fibrilla) which could be obtained; *d*, dim bands; *b*, bright bands, in the midst of each of which is seen the granular line *g*.

fined. In neither case can any distinct line of demarcation between a superficial layer and a deeper substance be recognised. The fibre appears transversely striped, as if the clear glassy substance were, at regular intervals (Fig. 88, A, *d*), converted into ground glass, thus appearing dimmer. Each of these "dim bands" is about 2μ wide, and the clear space or "bright band" which separates every two dim bands is of about the same size,

or under ordinary circumstances somewhat narrower. With a high power a very thin dark granular line equidistant from each dim band is discernible in each bright band, dividing the bright band into two. As these appearances remain when the object glass is focused through the whole thickness of the fibre, it follows that the dim bands, the granular lines, and the clear spaces on each side of each granular line, represent the edges of segments of different optical characters, which regularly alternate through the whole length of the fibre. Let the excessively thin segments, of which the thin granular lines represent the edges, be called *g*, the thicker, pellucid segments of which the bright bands on each side of a granular line represent the edges, B; and the thickest slightly opaque segments of which the ground glass like dim bands are the edges, D. Then the structure of the fibre may be represented by *D. B. g. B. D. B. g. B.* indefinitely repeated, and one inch of length of fibre will contain about 30,000 such segments, or alternations of structure.

In a perfectly unaltered living fibre the striated substance presents hardly any sign of longitudinal striation; but near to the surface of the fibre in mammalian muscle, though at various points in the depth of the fibre in the muscles of the frog, faint indications are to be observed of the existence of cavities each filled by a nucleus, surrounded by a small amount of protoplasm (Fig. 88, A, *n*).

As the muscular fibre dies it undergoes a rapid alteration :—(i) parallel longitudinal striæ, often less than 2μ apart, appear, in greater or less numbers until sometimes the striated substance appears broken up into a mass of fine delicate fibres; (ii) the dim bands become much more opaque, and hence the transverse striation appears better marked, until the dim bands may appear like sharply defined discs; (iii) the nuclei acquire sharp irregular contours and become much more conspicuous, and (iv) especially under certain circumstances and after particular

treatment, a thin superficial layer becomes sharply separated from the deeper substance of the fibre as a membrane of glassy transparency, the **sarcolemma**, which ensheathes the striated and fibrillated substance.

The bright bands and the granular lines, on the other hand, undergo little alteration.

Under very high powers each granular line looks like a number of minute granules lying side by side as an extremely thin plate, the margins of which are attached to the sarcolemma; it is often spoken of as *Krause's membrane*.

FIG. 89.—A MUSCULAR FIBRE (OF FROG) ENDING IN TENDON.

The striated muscular substance, *m*, has shrunk from the sarcolemma, *s*, the fibrils of the tendon, *t*, being attached to the latter.

If the sarcolemma of a dead fibre be torn with needles, the striated substance breaks up in different ways according to the treatment to which the fibre has been previously subjected. It may break up into discs, each of which contains a dim band. Or it may break up into fibrils, each of which presents the same segmentation as the whole fibre. These artificial fibrils vary much in thickness according to mode of preparation and the skill of the operator; they may sometimes be obtained of exceeding fineness (Fig. 88, B). Transverse sections of muscular fibre, which have been frozen while perfectly fresh, present minute close-set circular dots, which appear to represent the transverse sections of bundles of naturally existing longitudinal fibrils. These dots are known as **Cohnheim's areas.** If the muscle substance is really in this case unaltered the only possible interpretation of the fact is that the fibre is really made up of fibrils, and that these are invisible in the living muscle on account of their having the same refractive power as the interfibrillar sub-

stance. But whether the finest artificial fibrils into which dead muscle may be broken up are identical with these apparently natural fibrils, it is not at present certainly determined. In some cases the artificial fibrils seem smaller than the natural ones, as if the latter, like the fibre itself, were capable of longitudinal cleavage.

These are the most important structural appearances presented by ordinary striated muscle. But it may further be noticed that the dim bands exert a powerful influence on polarised light. Hence when a piece of muscle is placed in the field of a polarising microscope and the prisms are crossed so that the field is dark, these bands appear bright. The granular lines have a similar but very much less marked effect.

In the embryo the place of the adult tissue is occupied by a mass of closely applied, undifferentiated nucleated cells. As development proceeds, some of these cells are converted into the tissues of the perimysium, but others increasing largely in size gradually elongate and take on the form of more or less spindle-shaped rods or fibres. Meanwhile the nucleus of each cell repeatedly divides, and thus each rod becomes provided with many nuclei, so that each fibre is really a multi-nucleate cell. Along with these changes the protoplasmic substance of the original cell becomes, for the most part, converted into the characteristically striated muscle substance, only a little remaining unaltered around each nucleus as a muscle corpuscle.

The many-nucleated cell thus changed into a muscular fibre is nourished by the fluid exuded from the adjacent capillaries, and it may be said to respire, insomuch as its substance undergoes slow oxidation at the expense of the oxygen contained in that fluid, and gives off carbonic acid. It is, in fact, like the other elements of the tissues, an organism of a peculiar kind, having its life in itself, but dependent for the permanent maintenance of that life upon the condition of being associated with other

such elementary organisms, through the intermediation of which its temperature is kept constant and its supply of nourishment maintained.

The special property of a living muscular fibre, that which gives it its physiological importance, is its peculiar contractility. The body of a colourless blood corpuscle, as we have seen, is eminently contractile, insomuch as it undergoes incessant changes of form. But these changes take place at all points of its surface, and have no definite relation to the diameter of the corpuscle, while the contractility of the muscular fibre is manifested by a diminution in the length and a corresponding increase in the thickness of the fibre. Moreover, under ordinary circumstances, the change of form is effected very rapidly, and only in consequence of the application of a stimulus.

When a contracting striated fibre is observed under the microscope all the bands become broader (across the fibre) and shorter (along the fibre) and thus more closely approximated. Some observers think that the clear bands are diminished in total bulk relatively to the dim bands; but this is disputed by others. When the fibre relaxes again the bands return to their previous condition.

5. The Chemistry of Muscle.—Whilst much in the chemistry of muscle is obscure the muscular contraction may be compared to an explosion, the explosive material for which is manufactured on the spot. The muscle may therefore be regarded as consisting of (1) the stored explosive material, which is relatively small in quantity, (2) the machinery and fuel for its manufacture, and (3) the fabric of the building which forms the factory. Of these three the last is protein in nature, the other two we may consider as non-nitrogenous.

We are quite uncertain as to the actual nature of the explosion, *i.e.*, the physical and chemical changes which are directly associated with the change of shape in the muscle. They appear capable of taking place in the absence of oxygen and under such circumstances there would be little or no

evolution of heat or of carbonic acid, but the muscle would become acid in reaction due to the production of lactic acid. The obvious chemical changes which usually accompany the contraction of muscle are those involved in the manufacture of fresh explosive material. This material is a store of energy and is rebuilt at the expense of the active oxidation of other substances, of which probably sugar is usually the most important. The evidence of this oxidation consists of (1) the using up of sugar from the blood, (2) the using up of oxygen from the blood, (3) the discharge of carbonic acid into the blood, (4) the evolution of heat. When the supply of oxygen and nourishment to the muscle is sufficient, and the exercise is not excessive as in the case of the heart beating with its normal rhythm, there is no reason to suppose that any considerable quantity of acid such as lactic acid leaves the muscle.

In the absence of oxygen, or in the presence of a deficient supply of oxygen the reaction of the muscle becomes more acid, and this acidity has an effect on what we have spoken of as the protein fabric of muscle. At first this becomes less mobile, so that the muscle contracts with greater difficulty and under these conditions we say that the muscle is fatigued—a condition which must be distinguished from nervous fatigue or partial loss of "grip" over our muscles. Ultimately, if the muscle were persistently deprived of oxygen, the acid reaction would become so pronounced as to cause actual precipitation of the protein fabric; the muscle would then become opaque and lose its contractility much as it does when boiled. On stopping the circulation and thus cutting off the supply of oxygen these changes take place rapidly if the muscle is stimulated, slowly if it is not. In either case they spell death to the muscle and are a constant phase of the death of the individual. This coagulation of the protein fabric of the muscle on death is known as "**rigor mortis.**"

After the lapse of a certain time the coagulated matter liquefies, and the muscles pass into a loose and flabby condition, which marks the commencement of putrefaction.

If a muscle taken perfectly fresh from the body be cooled down with ice in order to keep it from undergoing change (just as was previously done with blood, p. 107) and subjected to considerable pressure it yields a fluid called **muscle plasma**. This remains fluid so long as it is kept adequately cooled, but *clots* spontaneously at ordinary temperatures, and may be made to clot when cold by the addition of small quantities of acid. This clotting results in the formation of a semi-solid gelatinous substance, called **myosin**, and a small amount of fluid, or **muscle serum**. Myosin is a protein and belongs to the same class of proteins as do the fibrinogen and paraglobulin of blood, namely the *globulins*.

Besides myosin, muscle contains other varieties of protein material about which we at present know little; a variable quantity of fat; certain inorganic saline matters, phosphates and potash being, as is the case in the red blood-corpuscles, in excess; and a large number of substances existing in small quantities, and often classed together as "extractives." Some of these extractives contain nitrogen; the most abundant of this class is **creatine**. It has been inferred that creatine is converted into urea, the most abundant waste product of the body, but of this there is no proof.

The other class of extractives contains bodies free from nitrogen, perhaps the most important of which are **sarcolactic acid** and **glycogen**.

Most muscles are of a deep, red colour; this is due in part to the blood remaining in their vessels; but only in part, for each fibre (into which no capillary enters) has a reddish colour of its own, like a blood-corpuscle but fainter. And this colour is probably due to the fibre possessing a small quantity of that same hæmoglobin in which the blood-corpuscles are so rich.

6. The Phenomena of Muscular Contraction.—Every fibre in a muscle has the property, under certain conditions of shortening in length, while it increases correspondingly in width, so that the volume of the fibre remains unchanged. This property is called **muscular contractility**, and whenever, in virtue of this property, a muscle fibre contracts it tends *to bring its two ends closer together*. Since a muscle is made up of a collection of these fibres, when the fibres contract the muscle as a whole also contracts ; it becomes shorter and thicker, and brings its two ends closer together, along with whatever may be fastened to those ends. By this action the muscles lead to the *motion* of the parts to which they are attached and by these motions give rise to *locomotion*.

The condition which ordinarily determines the contraction of a muscular fibre is, the passage along the nerve fibre, which is in close anatomical connection with the muscular fibre, of a **nervous impulse**, *i.e.*, of a particular change in the substance of the nerve which is propagated from particle to particle along the fibre. The nerve fibre is thence called a **motor fibre**, because, by its influence on a muscle, it becomes the indirect means of producing motion (see Lesson XI.).

The phenomena of muscular contraction may be conveniently studied in the muscles from the calf of a frog's leg, which, since the frog is a "cold-blooded" animal, retains its powers of contracting for some time after it is removed from the body. This muscle is called the **gastrocnemius** and may be dissected out so as to be still attached to a piece of the *femur* near the knee and to the nerve, the **sciatic**, which supplies it. This muscle as thus taken out of the body is known as a *muscle-nerve preparation* (Fig. 90).

The muscle may now be suspended by the femur and a weight hung on to the tendon at its lower end, and then made to contract by stimulating the sciatic nerve (see also Lesson XI.).

When the nerve is stimulated by a stimulus which lasts as short a time as possible, as, for instance, by the momentary electric current often called an induction shock, the following changes take place in the muscle.

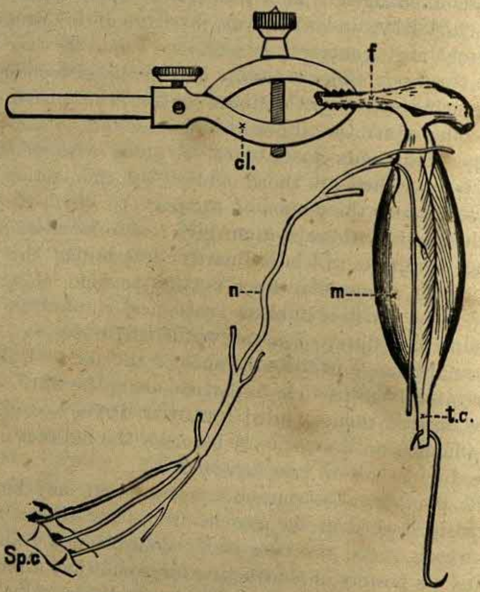

FIG. 90.—A MUSCLE NERVE PREPARATION.

m, the muscle, gastrocnemius of frog; *sp.c*, lower end of spinal column; *n*, the sciatic nerve, all the branches being cut away excepting that supplying the muscle; *f*, the femur; *cl.* a clamp to hold the femur; *t.a*, Achilles tendon.

(i) It becomes shorter and thicker, lifts the weight attached to it and then relaxes, allowing the weight to fall again. The shortening and relaxing takes place very rapidly, the whole process occupying rather more than $\frac{1}{10}$ of a second.

(ii) The muscle may be enclosed in a small chamber free from oxygen and made to contract several times. If now we examine the gas in the chamber in which this *excised* muscle has been contracting we cannot obtain satisfactory evidence of any escape of carbonic acid from the muscle during its contraction. That, however, the muscle *within the body richly supplied with oxygen* does give off carbonic acid during its contraction is clearly shown by the fact that the venous blood coming from a contracting muscle contains relatively more carbonic acid than it does when the muscle is at rest.

(iii) The muscle becomes slightly warmer; this can only be due to the fact that heat is formed during the contraction. The rise of temperature is slight, but may always be observed. The evolution of heat, like the oxidation processes with which it is associated, is probably associated with the formation, after the contraction, of fresh contractile material.

(iv) The muscle undergoes certain electrical changes. At the moment of commencing contraction the muscle becomes like a small battery cell, and can send an electric current through a wire whose ends are suitably applied to the surface of the muscle.[1]

7. The Tetanic Contraction of Muscles.—When experimenting with a muscle-nerve preparation, as in the preceding section, it is easy to stimulate the nerve twice in such rapid succession that the second stimulus is given while the muscle is in a state of contraction resulting from the first. In this case the muscle responds to the second stimulus as well as to the first; in other words it contracts still more while already contracting. The second contraction takes place on top of the first, is rather less in amount than the first, and is added on to the first. If now a *rapidly successive series of stimuli* be

[1] See also Lesson XI., where the electrical changes of an active nerve, which are essentially the same as those of a contracting muscle, are described in greater detail.

applied to the nerve, the muscle responds by an equally rapid series of contractions, each of which takes place before the preceding one is over; the whole series is thus added together, and the muscle remains in a state of *continued contraction* as long as the stimuli are continued, until exhaustion sets in. A prolonged contraction made up of such a series of single contractions superadded to each other is called a **tetanic contraction.** The acidity and heat which are developed at a single contraction become much more obvious during a continued tetanic contraction.

The voluntary contractions by which we execute the various movements of our body are in reality, in at all events nearly all cases, tetanic contractions, however short they may appear to be. Thus when we contract one of our muscles by an effort of the will it appears that a series of impulses is sent out in rapid succession from the spinal cord, perhaps at the rate of twelve or more in a second, to throw the muscle into prolonged contraction. By this means our control of the resulting movement is far greater than it would be if we were only able to execute single, short and sudden contractions such as result from sending a single impulse along the nerve going to the muscle.

8. The Various Kinds of Muscles.—Muscles may be conveniently divided into two groups, according to the manner in which the ends of their fibres are fastened; into muscles not attached to solid levers, and muscles attached to solid levers.

Muscles not attached to solid Levers.—Under this head come the muscles which are appropriately called **hollow** muscles, inasmuch as they inclose a cavity or surround a space; and their contraction lessens the capacity of that cavity, or the extent of that space.

The muscular fibres of the heart, of the blood-vessels, of the lymphatic vessels, of the alimentary canal, of the urinary bladder, of the ducts of the glands, of

the iris of the eye, are so arranged as to form hollow muscles.

In the heart the muscular fibres which, though peculiar are striated, are arranged in an exceedingly complex manner round the several cavities, and they contract, as we have seen, in a definite order.

The iris of the eye is like a curtain, in the middle of which is a circular hole. The muscular fibres are of the smooth or unstriated kind (see p. 288), and they are disposed in two sets: one set radiating from the edges of the hole to the circumference of the curtain; and the other set arranged in circles, concentrically with the aperture. The muscular fibres of each set contract suddenly and together, the radiating fibres necessarily enlarging the hole, the circular fibres diminishing it.

In the alimentary canal the muscular fibres are also of the unstriated kind, and they are disposed in two layers; one set of fibres being arranged parallel with the length of the intestines, while the others are disposed circularly, or rather at right angles to the former.

As has been stated above (p. 254), the contraction of these muscular fibres is successive; that is to say, all the muscular fibres, in a given length of the intestines, do not contract at once, but those at one end contract first, and the others follow them until the whole series have contracted. As the order of contraction is, naturally, always the same, from the upper towards the lower end, the effect of this peristaltic contraction is, as we have seen, to force any matter contained in the alimentary canal, from its upper towards its lower extremity. The muscles of the walls of the ducts of the glands have a substantially similar arrangement. In these cases the contraction of each fibre is less sudden and lasts longer than in the case of the heart.

Muscles attached to definite levers.—The great majority of the muscles in the body are attached to distinct levers, formed by the bones. In such bones as

FIG. 91.—LONGITUDINAL SECTION OF THE SHAFT OF A HUMAN FEMUR OR THIGH-BONE.

a, the head, which articulates with the haunch-bone; *b*, the medullary cavity, and *d*, the dense bony substance of the shaft; *c*, the part which enters into the knee-joint, articulating with the shin-bone, or tibia.

are ordinarily employed as levers, the osseous tissue is arranged in the form of a **shaft** (Fig. 91 *d.*), formed of a

very dense and compact osseous matter, but often containing a great central cavity (*b*) which is filled with a very delicate vascular and fibrous tissue loaded with fat called **marrow**. Towards the two ends of the bone, the compact matter of the shaft thins out, and is replaced by a much thicker but looser sponge-work of bony plates and fibres, which is termed the **cancellous** tissue of the bone. The surface even of this part, however, is still formed by a thin sheet of denser bone.

At least one end of each of these bony levers is fashioned into a smooth, articular surface, covered with cartilage, which enables the relatively fixed end of the bone to play upon the corresponding surface of some other bone with which it is said to be *articulated* (see p. 319), or, contrariwise, allows that other bone to move upon it.

It is one or other of these extremities which plays the part of fulcrum when the bone is in use as a lever.

Thus, in the accompanying figure (Fig. 92) of the bones of the upper extremity, with the attachments of the *biceps* muscle to the shoulder-blade and to one of the two bones of the fore-arm called the *radius*, P indicates the point of action of the power (the contracting muscle) upon the radius.

It usually happens that the bone to which one end of a muscle is attached is absolutely or relatively stationary; while that to which the other is fixed is movable. In this case, the attachment to the stationary bone is termed the **origin**, that to the movable bone the **insertion**, of the muscle.

The fibres of muscles are sometimes fixed directly into the parts which serve as their origins and insertions; but, more commonly, strong cords or bands of fibrous tissue, called **tendons**, are interposed between the muscle proper and its place of origin or insertion. When the tendons play over hard surfaces, it is usual for them to be separated from these surfaces by sacs containing fluid, which are called **bursæ**; or even to be invested by

synovial sheaths, *i.e.* quite covered for some distance by a synovial bag forming a double sheath, very much in the same way that the bag of the pleura covers the lung and the chest-wall.

Usually, the direction of the axis of a muscle is that of a straight line joining its origin and its insertion. But in some muscles, as the *superior oblique muscle* of the eye, the tendon passes over a pulley formed by ligament, and

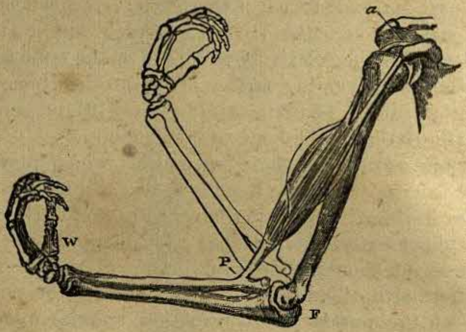

FIG. 92.—THE BONES OF THE UPPER EXTREMITY WITH THE BICEPS MUSCLE.

The two tendons by which this muscle is attached to the scapula are seen at *a*. P, indicates the attachment of the muscle to the radius, and hence the point of action of the power; F, the fulcrum, the lower end of the humerus on which the upper end of the radius (together with the ulna) moves; W, the weight (of the hand).

completely changes its direction before reaching its insertion. (See Lesson IX.)

Again, there are muscles which are fleshy at each end, and have a tendon in the middle. Such muscles are called *digastric*, or two-bellied. In the curious muscle which pulls down the lower jaw, and especially receives this name of *digastric*, the middle tendon runs through a pulley connected with the hyoid bone; and the muscle,

which passes downwards and forwards from the skull to this pulley, after traversing it, runs upwards and forwards to the lower jaw (Fig. 93).

9. The General and Minute Structure of Bone.—A fresh long bone such as the femur and humerus of a rabbit, from which the attached muscles, tendons and ligaments have been carefully cleaned away, but the surface of which has not been scraped or otherwise injured, is an excellent subject for the study of bone. It is a hard tough body which is flexible and highly elastic within narrow limits, but readily breaks, with a clean

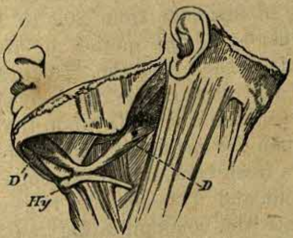

FIG. 93.—THE COURSE OF THE DIGASTRIC MUSCLE.

D, its posterior belly; D', its anterior belly; between the two is the tendon passing through its pulley connected with *Hy*, the hyoid bone.

fracture, if it is pressed too far. The two articular ends are coated by a layer of cartilage which is thickest in the middle. Where the margins of the cartilage thin out a layer of vascular connective tissue commences, and extending over the whole shaft, to the surface of which it is closely adherent, constitutes the **periosteum**. If the bone is macerated for some time in water, the periosteum may be stripped off in shreds with the forceps. Filaments pass from its inner surface into the interior of the bone. If the shaft is broken across it will be found to contain a

spacious **medullary cavity** filled by a reddish, highly vascular mass of connective tissue, abounding in fat cells, called the **medulla** or **marrow**; and a longitudinal section shows that this medullary cavity extends through the shaft, but in the articular ends becomes subdivided by bony partitions and breaks up into smaller cavities, like the areolæ of connective tissue. These cavities are termed **cancelli**, and the ends of the bone are said to have a *cancellated* structure. The walls of the medullary cavity in the shaft are very dense, and exhibit no cancelli and appear at first to be solid throughout. But on examining them carefully with a magnifying glass it will be seen that they are traversed by a meshwork of narrow canals, varying in diameter from 20μ to 100μ or more. The long dimensions of the meshes lie parallel with the axis of the shaft. These are the **Haversian canals**. This system of Haversian canals opens by short communicating branches on the one hand upon the periosteal and on the other upon the medullary surface of the wall of the shaft; and in a fresh bone, minute vascular prolongations of the periosteum and of the medulla respectively, may be seen to pass into the communicating canals and become continuous with the likewise vascular contents of the Haversian canals. Moreover, at one part of the shaft there is a larger canal through which the vessels which supply the medulla pass. This is the so-called **nutritive foramen** of the bone. At the two ends of the bone the cavities of the Haversian canals open into those of the cancelli; and the vascular substance which fills the latter thus further connects the vascular contents of the Haversian canals with the medulla.

Thus the bone may be regarded as composed of (i) an internal, thick, cylinder of vascular medulla; (ii) an external, hollow, thin, cylindrical sheath of vascular periosteum, completed at each end by a plate of articular cartilage; (iii) of a fine, regular, long-meshed vascular network which connects the sides of the medullary

cylinder with the periosteal sheath of the shaft ; (iv) of a coarse, irregular vascular meshwork occupying at each end the space between the medullary cylinder and the plate of articular cartilage, and connected with the periosteum of the lateral parts of the articular end ; (v) of the hard, perfect osseous tissue which fills the meshes of these two networks. Such is the general structure of all long bones with cartilaginous ends, though some, as the ribs, possess no wide medullary cavity, but are simply cancellated in the interior. In some very small bones even the cancelli are wanting. And there are many bones which have no connection with cartilage at all.

If a bone is exposed to a red heat for some time in a closed vessel nothing remains but a mass of white "bone-earth," which has the general form of the bone, but is very brittle and easily reduced to powder. It consists almost entirely of calcium phosphate and carbonate. On the other hand, if the bone is digested in dilute hydrochloric acid for some time the calcareous salts are dissolved out, and a soft, flexible substance is left, which has the exact form of the bone, but is much lighter. If this is boiled for a long time it will yield much gelatin, and only a small residue will be left. Osseous tissue therefore consists essentially of an animal matter impregnated with calcium salts, the animal matter being collagenous like connective tissue.

A sufficiently thin longitudinal section made by grinding down part of the wall of the medullary cavity of a bone—which has been well macerated in water and then thoroughly dried—if viewed as a transparent object with a magnifying glass, shows a series of lines, with dark enlargements at intervals, running parallel with the Haversian canals. If the section, instead of being longitudinal, were made transversely to the shaft, and therefore cutting through the majority of the Haversian canals at right angles to their length, similar lines and dark spots would be seen to form concentric circles at regular

intervals round each Haversian canal (Fig. 94). The hard bony tissue appears therefore to be composed of **lamellæ**, which are disposed concentrically around the Haversian canals; and a Haversian canal with the concentric lamellæ belonging to it form what is called a **Haversian system**. The soft substance from which the bone-earth has been extracted is similarly lamellated, and here and there presents fibres which may be traced into the fibrous substance of the periosteum.

If a thin section of dry bone is examined with the microscope (Fig. 95), by transmitted light, each dark spot is seen to be a black body (of an average diameter of about 15μ) with an irregular jagged outline, and proceeding from it are numerous fine dark lines which ramify in the surrounding matrix and unite with similar branched lines from adjacent black bodies. The matrix itself has a somewhat granular aspect. In a transverse section these black bodies are rounded or oval in form, but in a longitudinal section they appear almost spindle-shaped; that is to say they are lenticular or lens-shaped, but flattened as it were between the adjacent layers of the matrix. Examined by reflected light the same bodies look white and glistening; and if the section instead of being examined dry, be boiled in water or soaked in strong alcohol, and brought under the microscope while still wet, the black bodies with their branching lines will be found to have almost disappeared, only faint outlines of them being left. At the same time minute bubbles of air will have escaped from the section. The black bodies seen in the dry bone are in fact "**lacunæ**," *i.e.* gaps, or holes in the solid matrix, appearing black by transmitted light and white by reflected light, because they are filled with air; and the dark branched lines are similarly, minute canals, "**canaliculi**," also filled with air-bubbles, drawn out so to speak into lines, also hollowed out of the solid matrix, and placing one lacuna in communication with another. In each Haversian

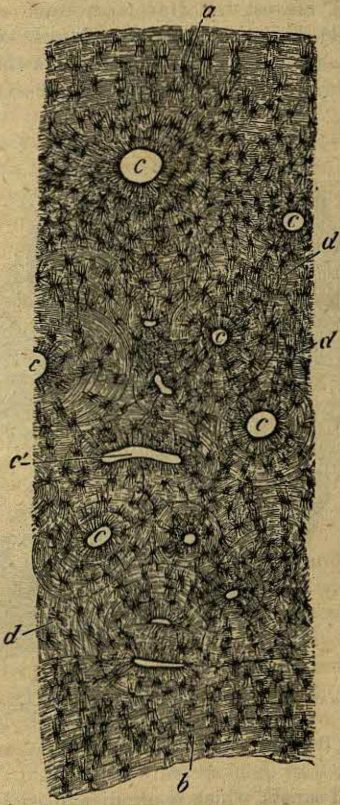

FIG. 94.—TRANSVERSE SECTION OF COMPACT BONE.

a, lamellae concentric with the external surface; *b*, lamellae concentric with the medullary surface; *c*, section of Haversian canals; *c′*, section of a Haversian canal just dividing into two; *d*, intersystemic lamellae. Low magnifying power.

system the *canaliculi*, and the *lacunæ* of the innermost layer or that nearest the Haversian canal communicate with it, while the *canaliculi* and the *lacunæ* of the outermost layer communicate only with those of the next inner layer. Hence the *lacunæ* and *canaliculi* compose a

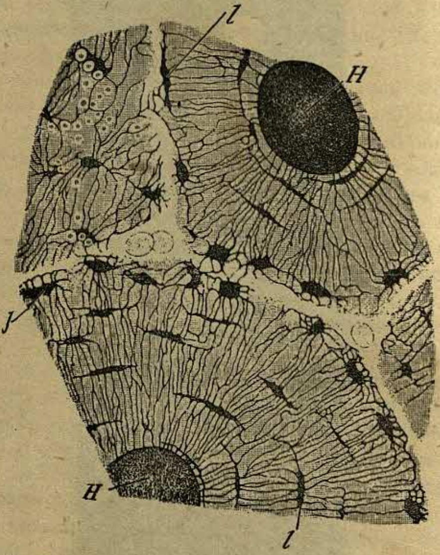

FIG. 95.—TRANSVERSE SECTION OF BONE, HIGHLY MAGNIFIED (300 DIAMETERS).

H, Haversian canals; *l*, lacunæ with canaliculi.

meshwork of canals, which is peculiar to each Haversian system, and by which the nutritive plasma exuded from the vessels in the canal of that system irrigates all the layers of bone which belong to the system.

A very thin section of perfectly fresh bone exhibits no dark bodies, inasmuch as the lacunæ and canaliculi con-

tain no air, but are permeated with the nutritive fluid. Each lacuna moreover, at all events in young bone, contains a nucleated cell, which is altogether similar in essential character to a connective tissue or cartilage corpuscle, and if the term were not already misused might be called a "**bone corpuscle.**" In fact, in ultimate analysis the essential character of bone shows itself to be this: that it is a tissue analogous to cartilage and connective tissue in so far as it consists of cells separated by much intercellular substance; and that it differs from them mainly in the fact that calcareous matter is deposited in and associated with the intercellular substance in such a way as to leave minute uncalcified passages (the *canaliculi*), which open into the larger uncalcified intervals (the *lacunæ*), in the neighbourhood of the cells.

The function of these passages is doubtless to allow of a more thorough permeation of the calcified tissue by the nutritive fluids than could take place if the calcareous deposit were continuous, and it is probable that, in an ordinary bone, there is no particle 1μ square which is not thus brought within reach of a minute streamlet of nutritive plasma.

This circumstance enables us to understand that which one would hardly suspect from the appearance of a bone, namely, that, throughout life, or, at all events, in early life, its tissue is the seat of an extremely active vital process. The permanence and apparent passivity of the bone are merely the algebraical summation of the contrary processes of destruction and reproduction which are going on in it.

If a young pig is fed with madder, its bones will be found after a time to be dyed red. The madder dye, in fact, getting into the blood, permanently dyes the tissue with which it meets in its course through the bones. But if the pig is fed for a time with madder, and is then deprived of it, the amount of colour to be found in the bones depends on the time which elapses before the

pig is killed. And it is not that the colouring matter is merely, as it were, washed out; the dye is permanent, but the bones nevertheless become parti-coloured. In the shaft of a long bone, for instance, a certain time after feeding with madder, a deep red layer of bone in the middle of thickness of its wall will be found to have colourless bone on its medullary and on its periosteal face. And the longer the time which has elapsed since the feeding with madder, the more completely will the deep red bone be replaced and covered up by colourless bone.

10. The Mechanics of Motion. The System of Levers.—To understand the action of the bones, as levers, properly, it is necessary to possess a knowledge of the different kinds of levers and be able to refer the various combinations of the bones to their appropriate lever-classes.

A lever is a rigid bar, one part of which is absolutely or relatively fixed, while the rest is free to move. Some one point of the movable part of the lever is set in motion by a force, in order to communicate more or less of that motion to another point of the movable part, which presents a resistance to motion in the shape of a weight or other obstacle.

Three kinds of levers are enumerated by mechanicians, the definition of each kind depending upon the relative positions of the point of support, or **fulcrum**; of the point which bears the resistance, **weight**, or other obstacle to be overcome by the force; and of the point to which the force, or **power** employed to overcome the obstacle, is applied.

If the fulcrum be placed between the power and the weight, so that, when the power sets the lever in motion, the weight and the power describe arcs, the concavities of which are turned towards one another, the lever is said to be of the **first order.** (Fig. 96, I.)

If the fulcrum be at one end, and the weight be between

it and the power, so that weight and power describe concentric arcs, the weight moving through the less space when the lever moves, the lever is said to be of the **second order.** (Fig. 96, II.)

And if, the fulcrum being still at one end, the power be between the weight and it, so that, as in the former case, the power and weight describe concentric arcs, but

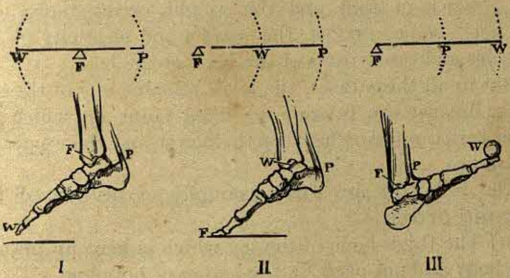

FIG. 96.

The upper three figures represent the three kinds of levers; the lower, the foot, when it takes the character of each kind.—W, weight or resistance; F, fulcrum; P, power.

the power moves through the less space, the lever is of the **third order.** (Fig. 96, III.)

In the human body the following parts present examples of **levers of the first order.**

(*a*) The skull in its movements upon the atlas, as *fulcrum.*

(*b*) The pelvis in its movements upon the heads of the thigh-bones, as *fulcrum.*

(*c*) The foot, when it is raised, and the toe tapped on the ground, the ankle-joint being *fulcrum.* (Fig. 96, I.)

The positions of the weight and of power are not given in either of these cases, because they are reversed according to circumstances. Thus, when the face is being

depressed, the power is applied in front, and the weight to the back part, of the skull; but when the face is being raised, the power is behind and the weight in front. The like is true of the pelvis, according as the body is bent forward, or backward, upon the legs. Finally, when the toes, in the action of tapping, strike the ground, the power is at the heel, and the resistance in the front of the foot. But when the toes are raised to repeat the act, the power is in front, and the weight, or resistance, is at the heel, being, in fact, the inertia and elasticity of the muscles and other parts of the back of the leg.

But in all these cases, the lever remains one of the first class, because the fulcrum, or fixed point on which the lever turns, remains between the power and the weight, or resistance.

The following are three examples of **levers of the second order**:—

(*a*) The thigh-bone of the leg which is bent up towards the body and not used, in the action of hopping.

For, in this case, the fulcrum is at the hip-joint. The power (which may be assumed to be furnished by the thick muscle[1] of the front of the thigh) acts upon the knee-cap; and the position of the weight is represented by that of the centre of gravity of the thigh and leg, which will lie somewhere between the end of the knee and the hip.

(*b*) A rib when depressed by the *rectus* muscle[2] of the abdomen, in expiration.

Here the fulcrum lies where the rib is articulated with the spine; the power is at the sternum—virtually the opposite end of the rib; and the resistance to be overcome lies between the two.

[1] This muscle, called *rectus*, is attached above to the haunch-bone and below to the knee-cap (Fig. 6, 2, p. 19). The latter bone is connected by a strong ligament with the *tibia*.

[2] This muscle lies in the front abdominal wall on each side of the middle line. It is attached to the sternum above and to the front of the pelvis below (Fig. 6, 8).

(*c*) The raising of the body upon the toes, in standing on tiptoe, and in the first stage of making a step forwards. (Fig. 96, II.)

Here the fulcrum is the ground on which the toes rest; the power is applied by the muscles of the calf to the heel (Fig. 6, I.); the resistance is so much of the weight of the body as is borne by the ankle-joint of the foot, which of course lies between the heel and the toes.

Three examples of **levers of the third order** are—

(*a*) The spine, head, and pelvis, considered as a rigid bar, which has to be kept erect upon the hip-joints. (Fig. 6.)

Here the fulcrum lies in the hip-joints, the weight is high above the fulcrum, at the centre of gravity of the head and trunk; the power is supplied by the extensor muscles (Fig. 6, 2) in the front of, or the flexor muscles (Fig. 6, II.) at the back of, the thigh, and acts upon points comparatively close to the fulcrum.

(*b*) Flexion of the forearm upon the arm by the **biceps** muscle, when a weight is held in the hand.

In this case, the weight being in the hand and the fulcrum at the elbow-joint, the power is applied at the point of attachment of the tendon of the biceps, close to the latter. (Fig. 92.)

(*c*) Extension of the leg on the thigh at the knee-joint.

Here the fulcrum is the knee-joint; the weight is at the centre of gravity of the leg and foot, somewhere between the knee and the foot; the power is applied by the muscles in front of the thigh (Fig. 6, 2 and Fig. 97), through the ligament of the knee-cap, or **patella,** to the tibia, close to the knee-joint.

In studying the mechanism of the body, it is very important to recollect that one and the same part of the body may represent each of the three kinds of levers, according to circumstances. Thus it has been seen that the foot may, under some circumstances, represent a lever of the first, in others, of the second, order. But it may

become a lever of the third order, as when one dances a weight resting upon the toes, up and down, by moving only the foot. In this case, the fulcrum is at the ankle-joint, the weight is at the toes, and the power is furnished by the extensor muscles at the front of the leg (Fig. 6, 1),

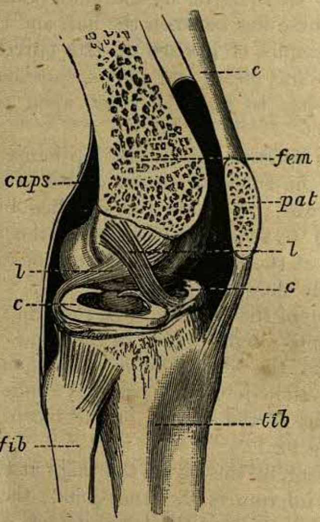

FIG. 97.—THE RIGHT KNEE-JOINT. THE OUTER HALF OF THE FEMUR AND PATELLA SAWN AWAY.

fem. femur; *pat.* patella; *tib.* tibia; *fib.* fibula; *caps.* capsule of joint; *l*, crucial ligaments; *c*, semilunar fibro-cartilages; *e*, tendon of extensor muscle.

which are inserted between the fulcrum and the weight. (Fig. 96, III.)

11. The Joints of the Body.—It is very important that the levers of the body should not slip, or work unevenly, when their movements are extensive, and to this end they

are connected together in such a manner as to form strong and definitely-arranged **joints** or **articulations.**

Joints may be classified into imperfect and perfect.

(*a*) **Imperfect joints** are those in which the conjoined levers (bones or cartilages) present no smooth surfaces, capable of rotatory motion, to one another, but are connected by continuous cartilages, or ligaments, and have only so much mobility as is permitted by the flexibility of the joining substance.

Examples of such joints as these are to be met with in the vertebral column—the flat surfaces of the bodies of the vertebræ being connected together by thick plates of very flexible fibro-cartilage, which confer upon the whole column considerable play and springiness, and yet prevent any great amount of motion between the several vertebræ. In the pelvis (see Plate, Fig. VI. and Fig. 4), the pubic bones are united to each other in front, and the iliac bones to the sacrum behind, by fibrous or cartilaginous tissue, which allows of only a slight play, and so gives the pelvis a little more elasticity than it would have if it were all one bone.

(*b*) In all **perfect joints**, the opposed bony surfaces which move upon one another are covered with cartilage, and between them is placed a sort of sac, which lines these cartilages, and, to a certain extent, forms the side walls of the joint; and which, secreting a small quantity of viscid, lubricating fluid—the **synovia**—is called **a synovial membrane.**

The opposed surfaces of these *articular* cartilages, as they are called, may be spheroidal, cylindrical, or pulley-shaped; and the convexities of the one answer, more or less completely, to the concavities of the other.

Sometimes, the two articular cartilages do not come directly into contact, but are separated by independent plates of cartilage, which are termed *inter-articular.* The opposite faces of these inter-articular cartilages are fitted to receive the faces of the proper articular cartilages.

While these co-adapted surfaces and synovial membranes provide for the free mobility of the bones entering into a joint, the nature and extent of their motion is defined, partly by the forms of the articular surfaces, and partly by the disposition of the **ligaments**, or firm, fibrous cords which pass from one bone to the other.

As respects the nature of the articular surfaces, joints may be what are called **ball and socket joints**, when the spheroidal surface furnished by one bone plays in a cup furnished by another. In this case the motion of the former bone may take place in any direction, but the extent of the motion depends upon the shape of the cup —being very great when the cup is shallow, and small in proportion as it is deep. The shoulder is an example of a ball and socket joint with a shallow cup (Fig. 5, B); the hip, of such a joint with a deep cup (Fig. 98).

Hinge-joints are single or double. In the former case, the nearly cylindrical head of one bone fits into a corresponding socket of the other. In this form of hinge-joint the only motion possible is in the direction of a plane perpendicular to the axis of the cylinder, just as a door can only be made to move round an axis passing through its hinges. The elbow is the best example of this joint in the human body, but the movement here is limited, because the **olecranon**, or part of the ulna which rises up behind the humerus, prevents the arm being carried back behind the straight line; the arm can thus be bent to, or straightened, but not bent back (Fig. 99). The knee (Fig. 97) and ankle present less perfect specimens of a single hinge-joint.

A double hinge-joint is one in which the articular surface of each bone is concave in one direction, and convex in another, at right angles to the former. A man seated in a saddle is "articulated" with the saddle by such a joint. For the saddle is concave from before backwards, and convex from side to side, while the man presents to it

the concavity of his legs astride, from side to side, and the convexity of his seat, from before backwards.

The metacarpal bone of the thumb is articulated with

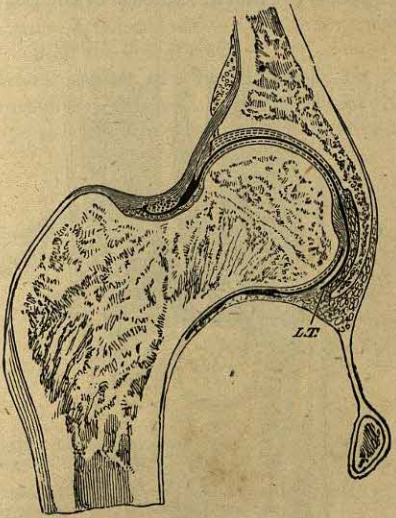

FIG. 98.—A SECTION OF THE HIP-JOINT TAKEN THROUGH THE ACETABULUM OR ARTICULAR CUP OF THE PELVIS AND THE MIDDLE OF THE HEAD AND NECK OF THE THIGH-BONE.

L.T, Ligamentum teres, or round ligament. The spaces marked with an interrupted line (- - - -) represent the articular cartilages. The cavity of the synovial membrane is indicated by the dark line between these, and, as is shown, extends along the neck of the femur beyond the limits of the cartilage. The peculiar shape of the pelvis causes the section to have the remarkable outline shown in the cut. This will be intelligible if compared with Fig. VI. in the plate.

the bone of the wrist, called *trapezium*, by a double hinge-joint.

A **pivot-joint** is one in which one bone furnishes an axis, or pivot, on which another turns; or itself turns on

its own axis, resting on another bone. A remarkable example of the former arrangement is afforded by the **atlas** and **axis**, or two uppermost vertebræ of the neck (Fig. 100). The axis possesses a vertical peg, the so-called **odontoid** process (*b*), and at the base of the peg are two,

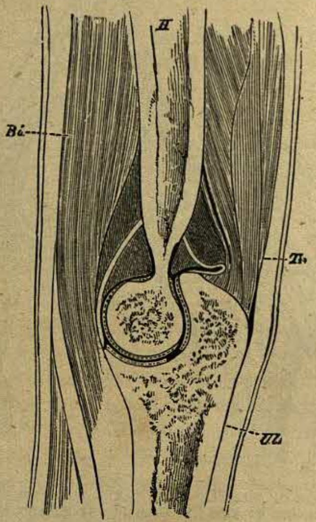

Fig. 99.- Longitudinal and Vertical Section through the Elbow-joint.

H, humerus; *Ul.* ulna; *Tr.* the *triceps* muscle, which extends the arm, *Bi*, the *biceps* muscle, which flexes it.

obliquely placed, articular surfaces (*a*). The atlas is a ring-like bone, with a massive thickening on each side. The inner side of the front of the ring plays round the neck of the odontoid peg, and the under surfaces of the lateral masses glide over the articular faces on each side of the base of the peg. A strong ligament passes between

the inner sides of the two lateral masses of the atlas, and keeps the hinder side of the neck of the odontoid peg in its place (Fig. 100, A). By this arrangement, the atlas is enabled to rotate through a considerable angle either way upon the axis, without any danger of falling forwards or backwards—accidents which would immediately destroy life by crushing the spinal cord.

The lateral masses of the atlas have, on their upper faces, concavities (Fig. 100, A, *a*) into which the two convex, occipital condyles of the skull fit, and in which they

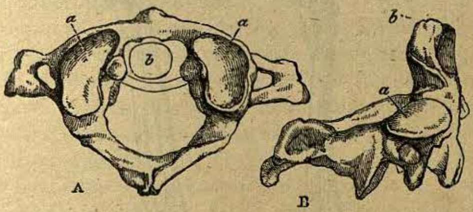

FIG. 100.

A. The atlas viewed from above; *a a*, upper articular surfaces of its lateral masses for the condyles of the skull; *b*, the peg of the axis vertebra.
B. Side view of the axis vertebra; *a*, articular surface for the lateral mass of the atlas; *b*, peg or odontoid process.

play upward and downward. Thus the nodding of the head is effected by the movement of the skull upon the atlas; while, in turning the head from side to side, the skull does not move upon the atlas, but the atlas slides round the odontoid peg of the axis vertebra.

The second kind of pivot-joint is seen in the forearm.

If the elbow and forearm, as far as the wrist, are made to rest upon a table, and the elbow is kept firmly fixed, the hand can nevertheless be freely rotated so that either the palm, or the back, is turned directly upwards. When the palm is turned upwards, the attitude is called

supination (Fig. 101, A); when the back, **pronation** (Fig. 101, B).

The forearm is composed of two bones; one, the **ulna**, which articulates with the **humerus** at the elbow by the hinge-joint already described, in such a manner that it can

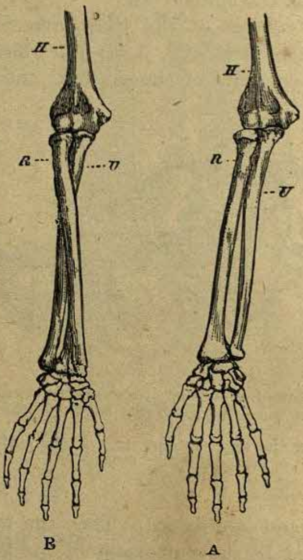

FIG. 101.

The bones of the right forearm in supination (A) and pronation (B). *H*, humerus; *R*, radius; *U*, ulna.

move only in flexion and extension (see p. 320), and has no power of rotation. Hence, when the elbow and wrist are rested on a table, this bone remains unmoved.

But the other bone of the forearm, the **radius**, has its small upper end shaped like a very shallow cup with thick

edges. The hollow of the cup articulates with a spheroidal surface furnished by the humerus: the lip of the cup, with a concave depression on the side of the ulna.

The large lower end of the radius bears the hand, and has, on the side next the ulna, a concave surface, which articulates with the convex side of the small lower end of that bone.

Thus the upper end of the radius turns on the double surface, furnished to it by the pivot-like ball of the humerus, and the partial cup of the ulna; while the lower end of the radius can rotate round the surface furnished to it by the lower end of the ulna.

In *supination*, the radius lies parallel with the ulna, with its lower end to the outer side of the ulna (Fig. 101, A). In *pronation*, it is made to turn on its own axis above, and round the ulna below, until its lower half crosses the ulna, and its lower end lies on the inner side of the ulna (Fig. 101, B).

The ligaments which keep the mobile surfaces of bones together are, in the case of ball and socket joints, strong fibrous *capsules* which surround the joint on all sides. In hinge-joints, on the other hand, the ligamentous tissue is chiefly accumulated, in the form of **lateral ligaments**, at the sides of the joints. In some cases ligaments are placed within the joints, as in the knee, where the bundles of fibres which cross obliquely between the femur and the tibia are called **crucial** ligaments (Fig. 97, *l*); or, as in the hip, where the **round ligament** passes from the bottom of the socket, or acetabulum of the pelvis to the ball furnished by the head of the femur (Fig. 98).

Again, two ligaments pass from the apex of the odontoid peg to both sides of the margin of the occipital foramen, *i.e.* the large hole in the base of the skull, through which the spinal cord passes to join the brain; these, from their function in helping to stop excessive rotation of the skull, are called **check ligaments** (Fig. 102, *a*).

In one joint of the body, the hip, the socket or **aceta-**

bulum (Fig. 98) fits so closely to the head of the femur, and the capsular ligament so completely closes its cavity on all sides, that the pressure of the air must be reckoned among the causes which prevent dislocation. This has been proved experimentally by boring a hole through the floor of the acetabulum, so as to admit air into its cavity, when the thigh-bone at once falls as far as the round and capsular ligaments will permit it to do, showing that it was previously pushed close up by the pressure of the external air.

12. The Various Movements of the Body.—The different kinds of movement which the levers thus connected are capable of performing are called **flexion** and **extension**; **abduction** and **adduction**; **rotation** and **circumduction.**

A limb is *flexed*, when it is bent; *extended*, when it is straightened out. It is *abducted*, when it is drawn away from the middle line; *adducted*, when it is brought to the middle line. It is *rotated*, when it is made to turn on its own axis; *circumducted*, when it is made to describe a conical surface by rotation round an imaginary axis.

No part of the body is capable of perfect rotation like a wheel, for the simple reason that such motion would necessarily tear all the vessels, nerves, muscles, &c., which unite it with other parts.

Any two bones united by a joint may be moved one upon another in, at fewest, two different directions. In the case of a pure hinge-joint, these directions must be opposite and in the same plane; but, in all other joints, the movements may be in several directions and in various planes.

In the case of a pure hinge-joint, the two practicable movements—viz., flexion and extension—may be effected by means of two muscles, one for each movement, and running from one bone to the other, but on opposite sides of the joint. When either of these muscles contracts, it will pull its attached ends together, and bend or straighten,

as the case may be, the joint towards the side on which it is placed. Thus the biceps muscle is attached, at one end, to the shoulder-blade, while, at the other end, its tendon passes in front of the elbow-joint to the radius (Figs. 92 and 99, *Bi*): when this muscle contracts, therefore, it bends, or flexes, the forearm on the arm. At the back of the joint there is the triceps (*Tr*, Fig. 99): when

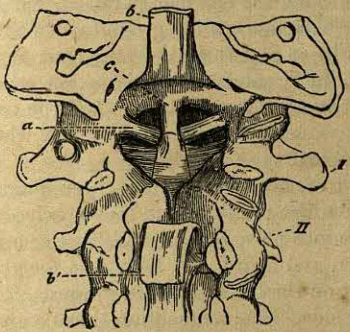

FIG. 102.

The vertebral column in the upper part of the neck laid open to show, *a*, the check ligaments of the axis; *b*, the broad ligament which extends from the front margin of the occipital foramen along the hinder faces of the bodies of the vertebræ; it is cut through, and the cut ends turned back to show, *c*, the special ligament which connects the point of the "odontoid" peg with the front margin of the occipital foramen; *I*, the atlas; *II*, the axis.

this contracts, it straightens, or extends, the forearm on the arm.

In the other extreme form of articulation—the ball and socket joint—movement in any number of planes may be effected, by attaching muscles in corresponding number and direction, on the one hand, to the bone which affords the socket, and on the other to that which furnishes the head. Circumduction will be effected by the combined and successive contraction of these muscles.

13. The Mechanics of Locomotion.—We may now pass from the consideration of the mechanism of mere motion to that of locomotion.

When a man who is standing erect on both feet proceeds to *walk*, beginning with the right leg, the body is inclined, so as to throw the centre of gravity forward; and, the right foot being raised, the right leg is advanced for the length of a step, and the foot is put down again. In the meanwhile, the left heel is raised, but the toes of the left foot have not left the ground when the right foot has reached it, so that there is no moment at which both feet are off the ground. For an instant, the legs form two sides of an equilateral triangle, and the centre of the body is consequently lower than it was when the legs were parallel and close together.

The left foot, however, has not been merely dragged away from its first position, but the muscles of the calf, having come into play, act upon the foot as a lever of the second order, and thrust the body, the weight of which rests largely on the left astragalus, upwards, forwards, and to the right side. The momentum thus communicated to the body causes it, with the whole right leg, to describe an arc over the right astragalus, on which that leg rests below. The centre of the body consequently rises to its former height as the right leg becomes vertical, and descends again as the right leg, in its turn, inclines forward.

When the left foot has left the ground, the body is supported on the right leg, and is well in advance of the left foot; so that, without any further muscular exertion, the left foot swings forward like a pendulum, and is carried by its own momentum beyond the right foot, to the position in which it completes the second step.

When the intervals of the steps are so timed that each swinging leg comes forward into position for a new step without any exertion on the part of the walker, walking is effected with the greatest possible economy of force.

And, as the swinging leg is a true pendulum—the time of vibration of which depends, other things being alike, upon its length (short pendulums vibrating more quickly than long ones),—it follows that, on the average, the natural step of short-legged people is quicker than that of long-legged ones.

In *running*, there is a period when both legs are off the ground. The legs are advanced by muscular contraction, and the lever action of each foot is swift and violent. Indeed, the action of each leg resembles, in violent running, that which, when both legs act together, constitutes a *jump*, the sudden extension of the legs adding to the impetus, which, in slow walking, is given only by the feet.

14. The Mechanism of the Larynx.—Perhaps the most singular motor apparatus in the body is the *larynx*, by the agency of which *voice* is produced.

The essential conditions of the production of the human voice are :—

(*a*) The existence of the so-called *vocal cords*.

(*b*) The parallelism of the edges of these cords, without which they will not vibrate in such a manner as to give out sound.

(*c*) A certain degree of tightness of the vocal cords, without which they will not vibrate quickly enough to produce sound.

(*d*) The passage of a current of air between the parallel edges of the vocal cords of sufficient power to set the cords vibrating.

The larynx is a short tubular box opening above into the bottom of the pharynx and below into the top of the trachea. Its framework is supplied by certain cartilages more or less movable on each other, and these are connected together by joints, membranes, and muscles. Across the middle of the larynx is a transverse partition, formed by two folds of the lining mucous membrane, stretching from either side, but not quite meeting in the

middle line. They thus leave, in the middle line, a chink or slit, running from the front to the back, called the **glottis**. The two edges of this slit are not round and flabby, but sharp and, so to speak, clean cut; they are also strengthened by a quantity of elastic tissue, the fibres of which are disposed lengthways in them. These sharp free edges of the *glottis* are the so-called **vocal cords**, or *vocal ligaments*.

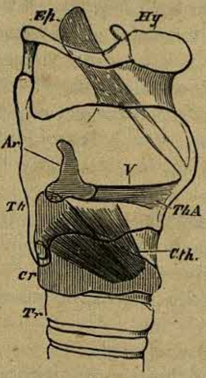

FIG. 103.

Diagram of the larynx, the thyroid cartilage (*Th*) being supposed to be transparent, and allowing the right arytenoid cartilage (*Ar*), vocal cords (*V*), and thyro-arytenoid muscle (*ThA*), the upper part of the cricoid cartilage (*Cr*), and the attachment of the epiglottis (*Ep*) to be seen. *C.th*, the right crico thyroid muscle; *Tr*, the trachea; *Hy*, the hyoid bone.

The **thyroid** cartilage (Fig. 103, *Th*) is a broad plate of gristle bent upon itself into a V shape, and so disposed that the point of the V is turned forwards, and constitutes what is commonly called "Adam's apple." Above, the thyroid cartilage is attached by ligament and membrane to the **hyoid** bone (Fig. 103, *Hy*). Below and behind, its broad sides are produced into little elongations or horns, which are articulated by ligaments with the outside of a great ring of cartilage, the **cricoid** (Fig. 103, *Cr*), which forms, as it were, the top of the windpipe.

The *cricoid* ring is much higher behind than in front, and a gap, filled up by membrane only, is left between its upper edge and the lower edge of the front part of the thyroid, when the latter is horizontal. Consequently, the thyroid cartilage, turning upon the articulations of its horns with the hinder part of the cricoid, as upon hinges, can be moved up and down through the space occupied by

this membrane; or, if the thyroid cartilage is fixed, the cricoid cartilage moves in the same way upon its articulations with the thyroid. When the thyroid moves downwards or the cricoid upwards, the distance between the front part of the thyroid cartilage and the back of the cricoid is necessarily increased; and when the reverse movement takes place the distance is diminished. There is, on each side, a large muscle, the **crico-thyroid**, which passes from the outer side of the cricoid cartilage obliquely upwards and backwards to the thyroid, and pulls the latter down; or, if the thyroid is fixed, pulls the cricoid up (Fig. 103, *C.th*).

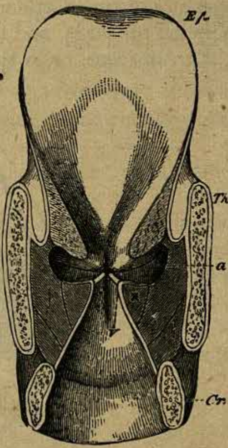

FIG. 104.—VERTICAL AND TRANSVERSE SECTION THROUGH THE LARYNX. THE HINDER HALF OF WHICH IS REMOVED.

Ep. Epiglottis; *Th.* thyroid cartilage; *a*, cavities called the *ventricles of larynx* above the vocal ligaments (*V*); × the right thyro-arytenoid muscle cut across; *Cr.* the cricoid cartilage.

Perched side by side upon the upper edge of the back part of the cricoid cartilage are two small irregularly-shaped but, roughly speaking, pyramidal cartilages, the **arytenoid** cartilages (Fig. 105, *Ary*). Each of these is articulated by its base with the cricoid cartilage by means of a shallow joint which permits of very varied movements, and especially allows the front portions of the two arytenoid cartilages to approach, or to recede from, each other.

It is to the forepart of one of these arytenoid cartilages that the hinder end of each of the two vocal ligaments is fastened; and they stretch from these points horizontally across the cavity of the larynx, to be attached, close to-

gether, in the re-entering angle of the thyroid cartilage rather lower than half-way between its top and bottom.

Now when the arytenoid cartilages diverge, as they do when the larynx is in a state of rest, it is evident that the aperture of the glottis will be V-shaped, the point of the V being forwards, and the base behind.

For, in front, or in the angle of the thyroid, the two

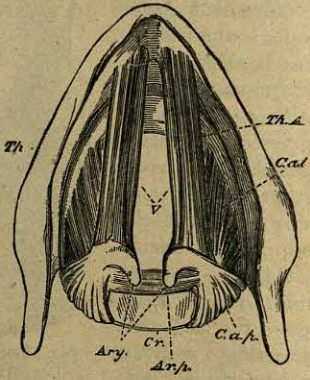

FIG. 105.—THE PARTS SURROUNDING THE GLOTTIS PARTIALLY DISSECTED AND VIEWED FROM ABOVE.

Th. the thyroid cartilage; *Cr.* the cricoid cartilage; *V*, the edges of the vocal ligaments bounding the glottis; *Ary*, the arytenoid cartilages; *Th.A*, thyro-arytenoid; *C.a.l.* lateral crico-arytenoid; *C.a.p*, posterior crico-arytenoid; *Ar.p*, posterior arytenoid muscles.

vocal ligaments are fastened permanently close together, whereas, behind, their extremities will be separated as far as the arytenoids, to which they are attached, are separated from each other. Under these circumstances a current of air passing through the glottis produces no sound, the parallelism of the vocal cords being wanting; whence it is that, ordinarily, expiration and inspiration take place quietly. Passing from one arytenoid cartilage to the

other, at their posterior surfaces are certain muscles called the **posterior arytenoid** (Fig. 105, *Ar.p.*). There are also two sets of muscles connecting each arytenoid with the cricoid, and called from their positions respectively the **posterior** and **lateral crico-arytenoid** (Fig. 105, *C.a.p. C.a.l.*). By the more or less separate or combined action of these muscles, the arytenoid cartilages, and especially the front part of these cartilages and, consequently, the hinder ends of the vocal cords attached to them, may be made to approach or recede from each other, and thus the vocal cords rendered parallel or the reverse.

We have seen that the crico-thyroid muscle pulls the thyroid cartilage down, or the cricoid cartilage up, and thus increases the distance between the front of the thyroid and the back of the cricoid, on which the arytenoids are seated. This movement, the arytenoids being fixed, must tend to pull out the vocal cords lengthways, or in other words to tighten them.

Running from the re-entering angle in the front part of the thyroid, backward, to the arytenoids, alongside the vocal cords (and indeed imbedded in the transverse folds, of which the cords are the free edges) are two strong muscles, one on each side (Fig. 105, *Th.A.*), called **thyro-arytenoid**. The effect of the contraction of these muscles is to pull up the thyroid cartilage after it has been depressed by the crico-thyroid muscles, (or to pull down the cricoid after it has been raised,) and consequently to slacken the vocal cords.

Thus the parallelism (*b*) of the vocal cords is determined chiefly by the relative distance from each other of the arytenoid cartilages; the tension (*c*) of the vocal cords is determined chiefly by the upward or downward movement of the thyroid or cricoid cartilage; and both these conditions are dependent on the action of certain muscles.

The current of air (*d*) whose passage sets the cords vibrating is supplied by the movements of expiration,

which, when the cords are sufficiently parallel and tense, produce that musical note which constitutes the voice, but otherwise give rise to no audible sound at all.

15. The Voice.—Voice consists simply of the sound, or musical note, which results from the vibration of the

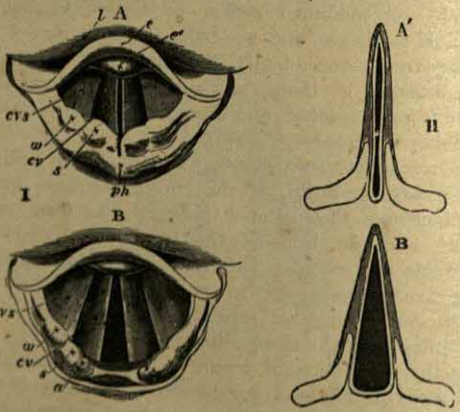

FIG. 106.

I. View of the human larynx from above as actually seen by the aid of the instrument called the laryngoscope; A, in the condition when voice is being produced; B, at rest when no voice is produced.

e. Epiglottis (foreshortened).

c.v. The vocal cords.

c.v.s. The so-called false vocal cords, folds of mucous membrane lying above the real vocal cords.

a. Elevation caused by the arytenoid cartilages.

s.w. Elevations caused by small cartilages connected with the arytenoids.

l. Root of the tongue.

II. Diagram of the same.

vocal cords. Other things being alike, the musical note will be low or high, according as the vocal cords are relaxed or tightened: and this again depends upon the relative predominance of the contraction of the crico-

thyroid and thyro-arytenoid muscles. For when the thyro-arytenoid muscles are fully contracted, the thyroid cartilage will be raised, relatively to the cricoid, as far as it can go, and the vocal cords will be rendered relatively lax; while, when the crico-thyroid muscles are fully contracted, the thyroid cartilage will be depressed, relatively to the cricoid, as much as possible, and the vocal cords will be made more tense.

If, while a low note is being sounded, the tip of the finger be placed on the crico-thyroid space (which can be felt, through the skin, beneath the lower edge of the thyroid cartilage), and a high note be then suddenly produced, the crico-thyroid space will be found to be narrowed by the approximation of the front edges of the cricoid and thyroid cartilages. At the same time, however, the whole larynx is, to a slight extent, moved bodily upwards and thrown forwards, and the cricoid has a particularly distinct upward movement; this movement of the whole larynx must be carefully distinguished from the motion of the thyroid relatively to the cricoid.

The **range** of any voice depends upon the difference of tension which can be given to the vocal cords, in these two positions of the thyroid cartilage. **Accuracy** of singing depends upon the precision with which the singer can voluntarily adjust the contractions of the thyro-arytenoid and crico-thyroid muscles—so as to give his vocal cords the exact tension at which their vibration will yield the notes required.

The **quality** of a voice—treble, bass, tenor, &c.—on the other hand, depends upon the make of the particular larynx, the primitive length of its vocal cords, their elasticity, the amount of resonance of the surrounding parts, and so on.

Thus, men have deeper notes than boys and women, because their larynxes are larger and their vocal cords longer—whence, though equally elastic, they vibrate less swiftly.

16. Speech.—Speech is voice modulated by the throat, tongue, and lips. Thus, voice may exist without speech; and it is commonly said that speech may exist without voice, as in whispering. This is only true, however, if the title of voice be restricted to the sound produced by the vibration of the vocal cords; for, in whispering, there is a sort of voice produced by the vibration of the muscular walls of the lips which thus replace the vocal cords. A whisper is, in fact, a very low whistle.

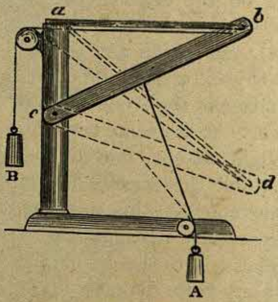

FIG. 107.

Diagram of a model illustrating the action of the levers and muscles of the larynx. The stand and vertical pillar represent the cricoid and arytenoid cartilages, while the rod (*b c*), moving on a pivot at *c*, takes the place of the thyroid cartilage; *a b* is an elastic band representing the vocal ligament. Parallel with this runs a cord fastened at one end to the rod *b c*, and, at the other, passing over a pulley to the weight B. This represents the thyro-arytenoid muscle. A cord attached to the middle of *b c*, and passing over a second pulley to the weight A, represents the crico-thyroid muscle. It is obvious that when the bar (*b c*) is pulled down to the position *c d*, the elastic band (*a b*) is put on the stretch.

The *modulation* of the voice into speech is effected by changing the form of the cavity of the mouth and nose, by the action of the muscles which move the walls of those parts.

Thus, if the pure vowel sounds—

E (as in *he*),	*A* (as in *hay*),	*A′* (as in *ah*),
O (as in *or*),	*O′* (as in *oh*),	*OO* (as in *cool*),

are pronounced successively, it will be found that they

may be all formed out of the sound produced by a continuous expiration, the mouth being kept open, but the form of its aperture, and the extent to which the lips are thrust out or drawn in so as to lengthen or shorten the distance of the orifice from the larynx, being changed for each vowel. It will be narrowest, with the lips most drawn back, in *E*, widest in *A′*, and roundest, with the lips most protruded, in *OO*.

Certain **consonants** also may be pronounced without interrupting the current of expired air, by modification of the form of the throat and mouth.

Thus the **aspirate**, H, is the result of a little extra expiratory force—a sort of incipient cough. *S* and *Z*, *Sh* and *J* (as in *jugular* = *G* soft, as in *gentry*), *Th*, *L*, *R*, *F*, *V*, may likewise all be produced by continuous currents of air forced through the mouth, the shape of the cavity of which is peculiarly modified by the tongue and lips.

All the vocal sounds hitherto noted so far resemble one another, that their production does not involve the stoppage of the current of air which traverses either of the modulating passages.

But the sounds of *M* and *N* can only be formed by blocking the current of air which passes through the mouth, while free passage is left through the nose. For *M*, the mouth is shut by the lips; for *N*, by the application of the tongue to the palate.

The other consonantal sounds of the English language are produced by shutting the passage through both nose and mouth; and, as it were, forcing the expiratory vocal current through the obstacle furnished by the latter, the character of which obstacle gives each consonant its peculiarity. Thus, in producing the consonants *B* and *P*, the mouth is shut by the lips, which are then forced open in this **explosive** manner. In *T* and *D*, the mouth passage is suddenly barred by the application of the point of the tongue to the teeth, or to the front part of the palate; while in *K* and *G* (hard, as in *go*) the middle and back of

the tongue are similarly forced against the back part of the palate.

An artificial larynx may be constructed by properly adjusting elastic bands, which take the place of the vocal cords ; and, when a current of air is forced through these, du regulation of the tension of the bands will give rise to all the notes of the human voice. As each vowel and consonantal sound is produced by the modification of the length and form of the cavities, which lie over the natural larynx, so, by placing over the artificial larynx chambers to which any requisite shape can be given, the various letters may be sounded. It is by attending to these facts and principles that various speaking machines have been constructed.

Although the tongue is credited with the responsibility of speech, as the "unruly member," and undoubtedly takes a very important share in its production, it is not absolutely indispensable. Hence, the apparently fabulous stories of people who have been enabled to speak, after their tongues had been cut out by the cruelty of a tyrant, or persecutor, may be quite true.

Some years ago I had the opportunity of examining a person, whom I will call Mr. R., whose tongue had been removed as completely as a skilful surgeon could perform the operation. When the mouth was widely opened, the truncated face of the stump of the tongue, apparently covered with new mucous membrane, was to be seen, occupying a position as far back as the level of the anterior pillars of the fauces. The dorsum of the tongue was visible with difficulty ; but I believe I could discern some of the circumvallate papillæ upon it. None of these were visible upon the amputated part of the tongue, which had been preserved in spirit ; and which, so far as I could judge, was about 2½ inches long.

When his mouth was open, Mr. R. could advance his tongue no further than the position in which I saw it ; but he informed me that, when his mouth was shut,

the stump of the tongue could be brought much more forward.

Mr. R.'s conversation was perfectly intelligible; and such words as *think*, *the*, *cow*, *kill*, were well and clearly pronounced. But tin became *fin*; tack, *fack* or *pack*; toll, *pool*; dog, *thog*; dine, *vine*; dew, *thew*; cat, *catf*; mad, *madf*; goose, *gooth*; big, pig, *bich*, *pich*, with a guttural *ch*.

In fact, only the pronunciation of those letters the formation of which requires the use of the tongue was affected; and, of these, only the two which involve the employment of its tip were absolutely beyond Mr. R.'s power. He converted all *t's*, and *d's* into *f's*, *p's*, *v's*, or *th's*. *Th* was fairly given in all cases; *s* and *sh*, *l* and *r*, with more or less of a lisp. Initial *g's* and *k's* were good; but final *g's* were all more or less guttural. In the former case, the imperfect stoppage of the current of air by the root of the tongue was of no moment, as the sound ran on into that of the following vowel; while, when the letter was terminal, the defect at once became apparent.

LESSON VIII

SENSATIONS AND SENSORY ORGANS

1. Movement the Result of Reflex Action.—The agent by which all the motor organs (except the cilia) described in the preceding Lesson are set at work, is muscular fibre. But, in the living body, muscular fibre is, as a rule, made to contract by a change which takes place in the **motor** or **efferent nerve**, which is distributed to it. This change again is generally effected by the activity of the **central nervous** system, with which the motor nerve is connected. The central organ is thrown into activity, directly or indirectly, by the influence of changes which take place in nerves, called **sensory** or **afferent**, which are connected, on the one hand, with the central organ, and, on the other hand, with some other part, usually on the surface, of the body. Finally, the alteration of the afferent nerve is itself produced by changes in the condition of the part of the body with which it is connected; which changes usually result from external impressions brought to bear on that part.

Sometimes the central organ enters into a state of activity without our being able to trace that activity to any direct influence of changes in afferent nerves; the activity seems to take origin in the central organ, and the movements to which it gives rise are called "spontaneous." Putting these cases on one side, it may be stated that a movement of the body or of a part of it, is to be regarded as the effect of an influence

(technically termed a **stimulus**) applied directly, or indirectly, to the ends of *afferent nerves*, and giving rise to a modification of the condition of the particles or *molecules* which form the substance of the nerve fibres, *i.e.*, to a **molecular change**, which is propagated from molecule to molecule along the fibres to the *central nervous system* with which these are connected. The molecular activity of the afferent nerve sets up changes of a like order in the fibres and cells of the central organ; from these the disturbance is transmitted along the *motor nerves*, which pass from the central organ to certain muscles. And, when the disturbance in the molecular condition of the efferent nerves reaches the endings of those nerves in muscular fibres, a similar disturbance is communicated to the substance of the muscular fibres, whereby, in addition to the production of certain other phenomena to some of which reference has already been made (Lesson VII.), the particles of the muscular substance are made to take up a new position, so that each fibre shortens and becomes thicker, and a movement ensues. Thus, for instance, if we *unintentionally* prick one of our fingers or touch some very hot object the hand is jerked away almost before we are aware of what has happened.

Such a series of molecular changes as that just described is called a **reflex action**: the disturbance in the afferent nerves caused by the irritation being as it were *reflected* back, along the efferent nerves, to the muscles. But the name is not a good one, since it seems to imply that the molecular changes in the afferent nerve, the central organ, and the efferent nerve are all alike, and differ only in direction; whereas there is reason to think that they differ in many ways.

The several structures necessary for the carrying out of a muscular contraction, resulting in movement, in the way we have described may be made clear by the following diagram.

The stimulus is applied to a sensory surface (*S*); the

change thus set up is propagated as a molecular disturbance (or impulse) along the sensory (afferent) nerve, *a.f.* to *c*, a part of the central nervous system (the spinal cord). The changes which then take place in *c* result in the setting up of a molecular disturbance in the motor (efferent nerve), *e.f.*, which is conveyed outwards along that nerve to the muscle M^1, usually on the same side of the body. Sometimes the impulse is sent out along a motor nerve to some muscle M^2 on the opposite side of the body.

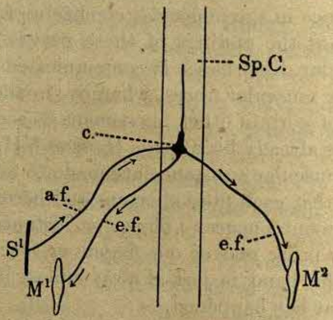

FIG. 108.—DIAGRAM TO ILLUSTRATE THE PATHS OF REFLEX ACTION.

Sp.c, spinal cord. *S*, some sensory surface; *a.f*, afferent or sensory nerve; *c*, central connection in nervous system; *e.f*, *e.f*, efferent or motor fibres; M^1, M^2, muscles. The arrows show the directions in which the impulses travel.

2. Sensations and Consciousness.—A reflex action may take place without our knowing anything about it, and hundreds of such actions are continually going on in our bodies without our being aware of them. But it very frequently happens that we learn that something is going on, when a stimulus affects our afferent nerves, by having what we call a *feeling* or **sensation.** We class sensations along with **emotions** and **volitions,** and

thoughts, under the common head of **states of consciousness.** But what consciousness is we know not; and how it is that anything so remarkable as a state of consciousness comes about as the result of irritating nervous tissue, is just as unaccountable as any other ultimate fact of nature.

Sensations are of very various degrees of definiteness. Some arise within ourselves, we know not how or where, and remain vague and undefinable. Such are the sensations of *uncomfortableness*, of *faintness*, of *fatigue*, or of *restlessness*. We cannot assign any particular place to these sensations, which are very probably the result of affections of the afferent nerves in general brought about by the state of the blood, or that of the tissues in which they are distributed. And however real these sensations may be, and however largely they enter into the sum of our pleasures and pains, they tell us absolutely nothing of the external world. They are not only *diffuse*, but they are also **subjective** sensations.

3. The Special Senses.—In the case of other sensations, each feeling arises out of changes taking place in a definite part of the body, is produced by a stimulus applied to that part of the body, and cannot be produced by stimuli applied to other parts of the body. Thus the sensations of **taste** and **smell** are confined to certain regions of the mucous membrane of the mouth and nasal cavities; those of **sight** and **hearing** to the particular parts of the body called the eye and the ear; and those of **touch**, though arising over a much wider area than the others, are nevertheless restricted to the skin and to some portions of the membranes lining the internal cavities of the body. Any portion of the body to which a sensation is thus restricted is called a **sense-organ.**

It may be here remarked that in the case of the sensation of touch, the simple feeling of contact is accompanied by information, not only as to what sense-organ, but also as to what part of that sense-organ, is being affected.

When we touch a hot or a rough body with the tip of a finger, we are aware not only that we are dealing with a hot or a rough body, but also that the hot or rough body is in contact with the tip of the finger; we "refer," as is said, the sensation to that part of the tip of the finger which is being acted upon by the body in question. With the other sensations the case is different. When we smell a bad smell, though we know that we smell by the nose, we do not consider that the smell arises in the nose; we conclude that there is some object outside ourselves which is causing the bad smell. We refer the origin of the sensation to some external cause, and that even when the sensation is after all due to changes taking place in the nose itself independently of external objects, as in the unpleasant odours which accompany certain diseases of the nose. Similarly all our sensations of sight and of hearing are referred to external objects; and even in the case of taste, when a lump of sugar is taken into the mouth, we are simply aware of a sensation of sweetness and do not associate that sensation of sweetness with any particular part of the mouth, though, by the sense of touch, which the inside of the mouth also possesses, we can tell pretty exactly whereabouts in the mouth the melting lump is lying.

4. The General Plan of a Sense-organ.—In these sensations, thus arising in special sense-organs, and hence often spoken of as "special" sensations, each sensation or feeling results from the application of a particular kind of stimulus to its appropriate sense-organ; and, in each case, the structure of the sense-organ is arranged in such a manner as to render that organ peculiarly sensitive to its appropriate stimulus.

Thus the sensations of sight are brought about by the action of the vibrations of the luminiferous ether; and the eye, or sense-organ of sight, is constructed in such a way that rays of light which falling on any other part of the body produce no appreciable effect, give rise to vivid sensations when they fall upon it.

We may distinguish in each sense-organ an **essential** and an **accessory** part.

The essential part of each sense-organ is composed of minute organs, which upon examination appear to be in reality modified epithelial cells ; and the delicate terminations of the nerve filaments distributed to the sense-organ may, with more or less distinctness, be traced to these modified cells, in which indeed they seem to end. These minute organs, these modified epithelial cells, may be spoken of as **sense-organules** ; they serve as intermediators in each case between the physical agent of the sensation and the sensory nerve. The physical agent is by itself unable to produce in the fibres of the sensory nerve those changes which, reaching the brain as nervous impulses, give rise to the special sensations. Thus, as we shall presently see, rays of light falling upon the optic nerve cannot give rise to a sensation of sight. The physical agent must act first on the sense-organules, and these in turn act upon the filaments of the nerve. Thus light falling upon the sense-organules, situated in that essential part of the eye called the retina, sets up changes in them, these changes set up corresponding changes in the delicate nerve filaments which with the sense-organules go to make up the retina, and the changes in the nerve filaments propagated along the optic nerve to the brain give rise, in the latter, to sensations of sight.

Hence in the essential part in each sense-organ we have to distinguish between the sense organules, *i.e.*, the modified epithelium, and the terminal expansion of the sensory nerve ; and further, in each sense-organ, there is added to this essential part a more or less complicated accessory part.

Lastly, in all these special sensations, there are certain phenomena which arise out of the structure of the sense-organ, and others which result from the operation of the central apparatus of the nervous system upon the materials supplied to it by the sense-organ.

5. The Skin as a Sense-Organ.—The sensations which originate in the skin and the parts which lie under it are those of pressure, heat, cold, and pain. These sensations are difficult to analyse.

Take for instance the sensation of pressure. If my hand is held out horizontally with the palm upwards and another person makes a considerable but unsuccessful effort to lower it by pressing the palm downwards, I can appreciate that pressure and even make an estimate of it. This I could do were there no skin on my hand. I am really appreciating the strain which is put upon my muscles and tendons in successfully resisting the pressure. The information is sent up to my brain from sense-organs situated in the tendons, muscles, and joints. In contrast to that experiment the following may be performed. The skin on the palm of my hand may be just touched lightly with a blunt object, or some cotton wool, and I may be asked if, without using my eyes, I can appreciate and locate the touch. In this experiment I am also appreciating sensations of pressure, but the sensations are quite different in kind as well as in degree from those estimated in the former experiment. The sense-organs which feel the cotton wool are in the skin. At once then we can divide our appreciation of pressure into two quite different faculties which are termed respectively the **deep** and the **superficial** sensibility according as they are located in the parts below the skin or in the skin itself.

Even in the skin however there seems to be more than one mechanism for the appreciation of any particular type of sensation (tactile sensation, heat, cold, or pain).

Just as in a microscope we have a "coarse" and "fine" adjustment for focussing the slide, so in the skin we have a coarse and a fine adjustment for the feeling of, say, pain. With the coarse adjustment only we get what we may speak of as a blurred image of pain, of heat or of

cold. We cannot be certain of the detail, small differences of temperature cannot be recognised, a prick is felt but the place where the prick was given is not known with certainty. We must not press the analogy of the microscope too far however. We might by accident obtain a clear vision of the slide without recourse to the fine adjustment of the microscope. No accident would produce for us detailed sensations without the corresponding mechanism in our skin.

For the trustworthy information which we possess on this subject we are indebted to the devotion of a physician who allowed the sensory nerve from part of the skin of his arm to be cut. The nerve grew again, and as the various sensations returned at different times, it was possible to distinguish between them. After about three months the rough as opposed to the detailed sensations come back, a rough appreciation of temperature and a rough sensation of pain—a thing which was really hot could be felt to be hot, a thing which was really cold could be felt to be cold, but he found it impossible to tell which was the hotter of two bodies which were nearly of the same temperature. To these rough sensations the name **protopathic** was given. The mechanism by which they are felt is that to which we have compared the coarse adjustment of the microscope. For a long time the skin had these sensations and these only. Then at a much later date, the delicate sensations returned—those of detailed touch, the ability to distinguish the contact of a single point from that of two points in close proximity, the power of appreciating small differences of temperature and the exact localisation of trifling pains, these sensations were called **epicritic**. The sensory end organs of these—both protopathic and epicritic—are situated in the skin.

Protopathic sensations, specially those of pain, are not confined to the skin but spread over a much greater

area; they are found, for instance, in the alimentary canal. Already we have said that a protopathic sensation may give the impression of coming from a different place from that at which it actually originates. This is especially true of sensations which come from the viscera. Such are often felt to be in the skin, indeed it is a remarkable thing that there are particular situations on the skin corresponding to various organs of the body so that a pain which really has its origin in the stomach will be felt always in one skin-area, whilst a pain from the kidney will be felt in another. This phenomenon is known as that of "**referred pain.**"

Let us turn to the structure of the skin to ascertain if possible the nature of the sensory end organs in it.

Whatever part possesses this sense consists of a membrane (integumentary or mucous) composed of a deep layer made up of fibrous tissue containing a capillary network, and of a superficial layer consisting of epithelial or epidermic cells, among which are no vessels.

Wherever the sense of touch is delicate, the deep layer is not a mere flat expansion, but is raised up into multitudes of small, close-set, conical elevations (see Fig. 57, p. 191), which are called **papillæ.** In the skin, the coat of epithelial or epidermic cells does not follow the contour of these papillæ, but dips down between them and forms a tolerably even coat over them. Thus, the points of the papillæ are much nearer the surface than the general plane of the deep layer whence these papillæ proceed. Loops of vessels enter the papillæ, and sensory nerve-fibres are distributed to them. In some cases the nerve-fibre ends in a papilla in a definite organ, in what is called a **tactile corpuscle**, or in a similar body called an **end-bulb.** Each of these organs consists essentially of an oval or rounded swelling formed by a modification and enlargement of the delicate connective tissue ensheathing

the nerve-fibre; in the middle of the swelling the nerve-fibre itself ends abruptly in a peculiar manner. These bodies are especially found in the papillæ of those localities which are endowed with a very delicate sense of touch, as in the tips of the fingers, the point of the tongue, &c.; and the papillæ which contain tactile corpuscles generally contain few or no blood-vessels.

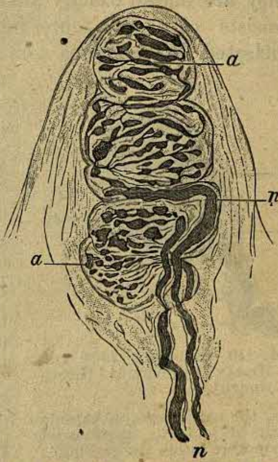

FIG. 109.—TACTILE CORPUSCLE WITHIN A PAPILLA OF THE SKIN OF THE HAND (RANVIER).

n.n, two nerve fibres passing to the corpuscle; *a.a*, varicose terminations of the nerve fibres inside the corpuscle.

Tactile corpuscles occur most numerously in the papillæ of the skin of the palmar surface of the hand, especially of the finger-tips; they are also present, but much less numerously, on the plantar surfaces of the skin of the toes, and are commonest on parts of the skin where there is no hair. Each corpuscle forms an elongated, bulbous swelling about 75μ ($\frac{1}{300}$ inch) in length at the end of the nerve-fibre to which it is attached, and lies with its long axis pointing to the top of the papilla. The corpuscle consists of a sheath or capsule of connective tissue inside of which are some nucleated cells intermixed with connective tissue derived from the outer sheath. The nerve which supplies the corpuscle approaches it at its side, winds once or twice round it and then enters the body of the corpuscle, where it divides

into a number of branches which end in a manner not as yet exactly determined.

End bulbs are found in the papillæ of the skin of the lips and in other situations. They are spheroidal and smaller (40μ in diameter) than the tactile corpuscles. They are not all exactly alike, but the commonest form consists of a thin outer sheath or capsule which is nucleated and encloses a mass of polygonal cells. The nerve-fibre enters the capsule and ends among the cells in its interior.

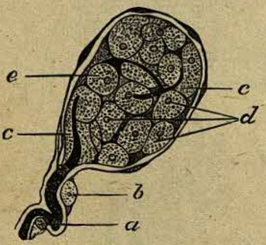

FIG. 110.—END-BULB FROM THE HUMAN CONJUNCTIVA[1] (LONGWORTH).

a, the nerve-fibre; *b*, capsule with nuclei; *c.c*, portions of nerve-fibre inside the end-bulb; *d.e*, cells of the core.

The great majority, however, of the nerve-fibres going to the skin do not end in any such definite organs. They divide in the dermis into exceeding delicate minute filaments, the course and ultimate terminations of which are traced with the greatest difficulty. Some of the finest filaments, however, pass into the epidermis and are there lost among or possibly connected with some of the epidermic cells, especially those of the lower layers.

Another kind of highly specialised nerve-ending is found on the branches of the nerves which supply the skin of the hand and foot, as they pass through the subcutaneous tissue. These are known as **Pacinian corpuscles**, called after Pacini, who first carefully described them. From their position they are not, strictly speaking, sensory endings of nerves in the skin; but they possess

[1] The conjunctiva is the mucous membrane which lines the eyelids and front of the eyeball.

undoubtedly some sensory functions, although we do not know what these may be.

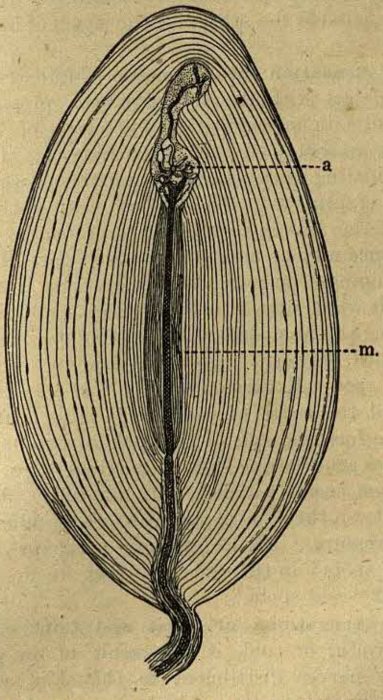

FIG. 111.—A PACINIAN CORPUSCLE FROM A CAT'S MESENTERY. (RANVIER.)

n, nerve-fibre, passing through the core *m*, and terminating at *a*.

The Pacinian corpuscles are long, oval, bulbous structures of considerable size, averaging $\frac{1}{10}$ of an inch in length. They are thus easily visible to the naked eye.

Each corpuscle consists of an elongated central core of glassy-looking material in which the axis of the nerve is embedded and terminates. The core is surrounded by some 30 to 40 capsules made of connective tissue, and placed one outside the other like the layers of an ordinary onion.

(i) **The Sensation of Pressure.**—Mere contact of a single object with the skin exerts a pressure on it which results in a stimulation by means of which we become aware that something is touching us. The power of discriminating pressure and its differences we may call the sense of pressure. The sensitiveness of the various regions of the skin in responding to pressure varies, and the difference may be measured for each part of the skin by determining either what the least weight is which can be just felt when allowed to rest on that part, or else by determining the least difference in weight which can be distinguished between two weights laid in succession on the same spot. Experimenting in this way it may be shown that the sense of pressure is most acute on the skin of the forehead and of the back of the hand. The sense is less acute in the skin of the finger tips. Careful investigation seems to show, with but little doubt, that some points on the skin of any part are peculiarly sensitive to pressure. Hence we may perhaps speak of "pressure spots" in the same way that we do of "heat spots" and "cold spots."

(ii) **The Sensations of Heat and Cold.**—The feeling of warmth, or cold, is the result of an excitation of sensory nerves distributed to the skin, which are possibly distinct from those which give rise to the sense of touch. And it would appear that the heat must be transmitted through the epidermic or epithelial layer, to give rise to this sensation ; for, just as touching a naked nerve, or the trunk of a nerve, gives rise only to pain, so heating or cooling an exposed nerve, or the trunk of a

nerve, gives rise not to a sensation of heat or cold, but simply to pain. Thus, if the elbow be dipped into a mixture of ice and salt, the cold first affects the skin of the elbow, giving rise to a sensation of cold at the elbow, but afterwards attacks the trunk of the ulnar nerve, which at the elbow lies not very far below the skin ; and this latter effect is felt as a sensation, not of cold, but of pain. The pain, moreover, thus caused is not felt in the trunk of the nerve at the elbow, where the cold is acting, but in the parts where the fibres of the nerve end, more particularly in the little and ring fingers.

Again, the sensation of heat, or cold, is relative rather than absolute. Suppose three basins be prepared, one filled with ice-cold water, one with water as hot as can be borne, and the third with a mixture of the two. If the hand be put into the hot-water basin, and then transferred to the mixture, the latter will feel cold ; but if the hand be kept a while in the ice-cold water, and then transferred to the very same mixture, this will feel warm.

Like the sense of touch, the sense of warmth varies in delicacy in different parts of the body. The cheeks are very sensitive, more so than the lips ; the palms of the hands are more sensitive to heat than their backs. Hence a washerwoman holds her flat-iron to her cheek to test the temperature, and one who is cold spreads the palms of his hands to the fire.

The differences in the sensitiveness of the skin to heat and cold at various points may be readily determined by touching the several points with the blunt end of a wire whose temperature can be kept constant at any desired degree. In this way it is found that some points respond to heat but not to cold, others to cold but not to heat, so that we meet with "heat spots" and "cold spots." The accompanying figure shows the distribution of these spots in a small area of the skin of the thigh.

(iii) **The Sensation of Pain.**—Pain may be regarded as the result of an excessive stimulation of any of the nerve endings which are concerned in giving rise to sensations. Pain also results from stimulating the trunks of the nerves leading from those endings to the central

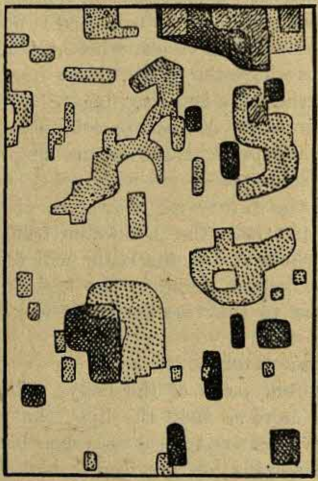

FIG. 112.—OUTLINES OF HEAT SPOTS AND COLD SPOTS. (AFTER GOLDSCHEIDER.)

The heat spots are cross-hatched and dark, the cold spots are dotted and light. In some places the heat spots and cold spots overlap each other.

nervous system. In the latter case the pain is "referred" outwards to the end of the nerve, as in the experiment of cooling the elbow described above. The nerves of any part may thus give rise to pain. From this it might appear that we can scarcely speak of any distinct and

separate "sense" of pain. But there are certain facts which show that sensations of pain are distinct from other sensations. In the first place there is a protopathic sensation of pain, in many places in which there is no such sensation of contact. Again there are certain situations in the body which are incapable of appreciating touch, but which readily feel pain, and in many diseases of the nervous system, such as locomotor ataxy, the sensitiveness of the skin to touch may be almost entirely wanting, while pain is readily felt. Further, observation shows that the impulses giving rise to pain, as also those resulting from heat and cold, pass along the spinal cord on their way to the brain by paths which are distinct from those which convey the impulses resulting from mere touch.

(iv) **The Localisation of Tactile Sensations.**—Certain very curious phenomena appertain to the sense of touch; some of these are probably in part due to varying anatomical arrangements, to the varying thickness of the epidermis, and to the abundance or scantiness of special end-organs. Not only is tactile sensibility to a single impression much duller in some parts than in others—a circumstance which might in many cases be accounted for by the different thickness of the epidermic layer—but the power of distinguishing double simultaneous impressions is very different. Thus, if the ends of a pair of compasses (which should be blunted with pointed pieces of cork) are separated by only one-tenth or one-twelfth of an inch, they will be distinctly felt as two, if applied to the tips of the fingers; whereas, if applied to the back of the hand in the same way, only one impression will be felt; and, on the arm, they may be separated for a quarter of an inch, and still only one impression will be perceived.

Accurate experiments have been made in different parts of the body, and it has been found that two points

can be distinguished by the tongue, if only one-twenty-fourth of an inch apart; by the tips of the fingers if one-twelfth of an inch distant; while they may be one inch distant on the cheek or forehead, and even three inches on the back, and still give rise to only one sensation.

Lastly, can we find any correspondence between the various forms of end organ which have been described and the various sensations felt in the skin? The epicritic sense of pressure is felt in many parts of the skin by tactile corpuscles (Fig. 109). This is especially the case where there are no hairs as on the palms of the hands. The nerve-endings attached to the small hairs serve the same function elsewhere. End-bulbs probably acquaint us with "cold." We are uncertain as to the corresponding organs for "heat."

6. **The Muscular Sense.**—What is termed the muscular sense is less vaguely localised than the sensations referred to above in Section 2 (p. 343), though its place is still incapable of being very accurately defined. This muscular sensation is largely the feeling of resistance which arises when any kind of obstacle is opposed to the movement of the body, or of any part of it; and it is something quite different from the feeling of contact or even of pressure.

Lay one hand flat on its back upon a table, and rest a disc of cardboard a couple of inches in diameter upon the ends of the outstretched fingers; the only result will be a sensation of **contact**—the pressure of so light a body being inappreciable. But put a two-pound weight upon the cardboard, and the sensation of *contact* will pass into what appears to be a very different feeling, viz., that of **pressure**. Up to this moment the fingers and arm have rested upon the table; but now let the hand be raised from the table, and another new feeling will make its appearance—that of **resistance to effort**. This

feeling comes into existence with the exertion of the muscles which raise the arm; and it is the consciousness of that exertion which goes by the name of "the muscular sense."

Any one who raises or carries a weight knows well enough that he has this sensation; but he may be greatly puzzled to say where he has it. Nevertheless, the sense itself is very delicate, and enables us to form tolerably accurate judgments of the relative intensity of resistances. Persons who deal in articles sold by weight are constantly enabled to form very precise estimates of the weight of such articles by balancing them in their hands; and in this case, they depend in a great measure upon the muscular sense.

But the muscular sense embraces more than the mere consciousness of the *resistance to effort* involved in lifting a weight. Thus it is a matter within everybody's experience that, even when the eyes are closed, we are perfectly well aware of the *direction and extent of any movement* of any part of the body. Moreover we are equally conscious of the *position* of any part of the body at any moment, whether the position is the result of our own voluntary movement or the result of the action of some other person who has placed the part in position. In all such cases the muscular sense supplies the basis of our knowledge of the position or of the movements of the parts of our body.

The muscular sense is thus essentially concerned with sensations arising from movements whether active or passive. Now the parts affected by these movements are chiefly the following three; the skin, the muscles and the tendons or ligaments. It has been supposed that the impulses which give rise to the sensations may be largely due to the stimulation of cutaneous nerves resulting from the varying extent to which the skin is put on the stretch by the movements; but the arguments in favour of this view are not conclusive. On the other hand we know

that the muscles themselves possess nerve fibres which are certainly afferent, *i.e.* sensory; and similarly afferent fibres, connected with extremely minute end-bulbs, are distributed to the tendons. And there is but little doubt that we must look to the impulses generated in these nerves, more especially the nerves of the tendons, as providing the sensations which form the basis of the muscular sense.

7. The Sense of Taste.—The organ of the sense of taste is the mucous membrane which covers the tongue, especially its back part, and the hinder part of the palate. Like that of the skin, the deep, or vascular, layer of the mucous membrane of the tongue is raised up into papillæ; but these are large, separate, and have separate coats of epithelium. Towards the tip of the tongue they are for the most part elongated and pointed, and are called **filiform**; over the rest of the surface of the tongue these are mixed with other large papillæ, with broad ends and narrow bases, called **fungiform**; but towards its root there are a number of larger papillæ, arranged in the figure of a V with its point backwards, each of which is like a fungiform papilla surrounded by a wall. These are the **circumvallate** papillæ (Fig. 113, *C.p.*). The larger of these papillæ have subordinate small ones upon their surfaces.

In both the fungiform and circumvallate papillæ, the cells which are specially concerned in giving rise to sensations of taste are arranged in bulbous groups, somewhat like the leaves in a bud, and hence these groups are known as **taste-buds**. In the circumvallate papillæ these taste-buds lie imbedded in the layers of epithelium which cover the sides of each papilla.

Each "bud" is flask-shaped and consists of an outer wall, made up of elongated cells placed side by side like the staves of a barrel, and leaving an opening at the end of the bud where it comes to the surface of the papilla. The inside of the bud is filled with the true **gustatory cells**,

packed side by side into the cavity of the bud. Each of these cells is long and very thin, with a large nucleus at its middle point, and each cell has at its outer end a

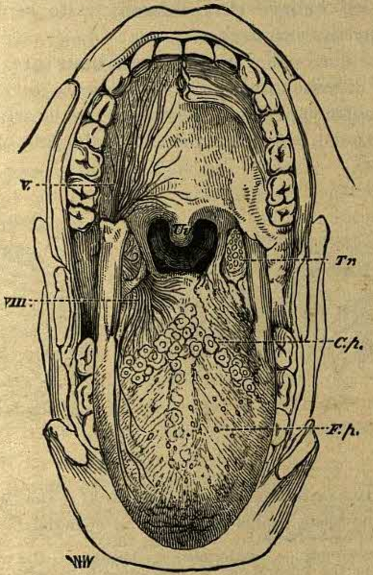

FIG. 113.—THE MOUTH WIDELY OPENEL TO SHOW THE TONGUE AND PALATE.

Uv. the uvula; *Tn.* the tonsil between the anterior and posterior pillars of the fauces; *C.p*, circumvallate papillæ; *F.p*, fungiform papillæ. The minute filiform papillæ cover the interspaces between these. On the right side the tongue is partially dissected to show the course of the filaments of the glossopharyngeal nerve, *VIII.*

delicate process, like a stiff cilium (but not vibratile), which projects through the open mouth of the bud.

The papillæ are very vascular, and they receive nervous filaments from two sources, the one the nerve called

glossopharyngeal, the other the **gustatory**, which is a branch of the **fifth** nerve (see Lesson XI.). The latter chiefly supplies the front of the tongue, the former its back and the adjacent part of the palate; and there is reason to believe that different taste sensations are supplied by the two nerves.

The peculiar cells in the taste-buds are the sense-organules of taste, and, with the delicate terminations of the glossopharyngeal and gustatory nerve which may be traced to them, constitute the *essential* parts of the organ

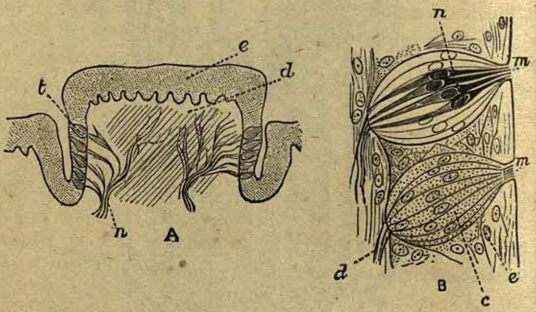

FIG. 114.—DIAGRAM OF A CIRCUMVALLATE PAPILLA, AND OF TASTE-BUDS.

A, A circumvallate papilla cut across; *e*, epidermis; *d*, dermis; *t*, taste-buds; *n*, nerve fibres.

B, Two taste buds; *e*, epidermis; *d*, dermis; *c*, the outer or cover cells shown in the lower bud; *n*, four inner cells with processes; *m*, processes projecting at mouth of buds.

of taste. The tongue itself, which by its movements brings the sapid substances into immediate contact with these modified epithelium cells, may be regarded as the accessory part.

The great majority of the sensations we call taste, however, are in reality complex sensations, into which smell, and even touch, and the temperature sense, as in the sensation of cold produced by peppermint, largely enter. When the sense of smell is interfered with, as when the

nose is held tightly pinched, it is very difficult to distinguish the taste of various objects. An onion, for instance, the eyes being shut, may then easily be confounded with an apple. This explains the not uncommon device of pinching the nose when taking nauseous medicine.

But the so-called "tastes" which are thus affected by the absence of smell ought rather to be spoken of as "flavours" than as tastes. They are distinctly due to the odoriferous particles the substances emit, and thus people are in the habit of "sniffing" a glass of wine in order to appreciate what they call its taste. True taste is independent of smell, as in the case of sugar or quinine. When we come to investigate the matter closely, we find that the various real tastes may be arranged under four heads: these are—sweet, bitter, sour or acid, and salt. These tastes are not excited equally all over the surface of the tongue. Thus the tip is most sensitive to sweet substances, and the back to bitter, while the sides of the tongue most readily respond to acids.

The sense of taste is most acute at medium temperatures, such as 20°—30° C. (68°—95° F.), and substances to be tasted must be in solution.

8. The Sense of Smell.—The organ of the sense of smell is the delicate mucous membrane which lines the upper part of the nasal cavities. In this part the mucous membrane is distinguished from the rest of the mucous membrane of these cavities—firstly, by the character of its cells and by possessing no cilia; secondly, by receiving a large nervous supply from the olfactory, or first, pair of cerebral nerves (see Lesson XI.), as well as a certain number of filaments of the fifth pair, whereas the rest of the mucous membrane is supplied from the fifth pair alone.

Each nostril leads into a spacious nasal chamber, separated, in the middle line, from its fellow of the other side, by a partition, or **septum**, formed partly by cartilage and partly by bone, and continuous with that partition

which separates the two nostrils one from the other. Below, each nasal chamber is separated from the cavity of the mouth by a floor, the bony palate (Figs. 115 and 116); and when this bony palate comes to an end, the partition is continued down to the root of the tongue by a fleshy curtain, the soft palate, which has been already described. The soft palate and the root of the tongue together, constitute, under ordinary circumstances, a movable partition between the mouth and the pharynx; and it will be observed that the opening of the larynx, the *glottis*, lies behind the partition; so that when the root of the tongue is applied close to the soft palate no passage of air can take place between the mouth and the pharynx. But in the upper part of the pharynx above the partition are the two hinder openings of the nasal cavities (which are called the **posterior nares**) separated by the termination of the septum; and through these wide openings the air passes, with great readiness, from the nostrils along the lower part of each nasal chamber to the glottis, or in the opposite direction. It is by means of the passages thus freely open to the air that we breathe, as we ordinarily do, with the mouth shut.

Each nasal chamber rises, as a high vault, far above the level of the arch of the posterior nares—in fact, about as high as the depression of the root of the nose. The uppermost and front part of its roof, between the eyes, is formed by a delicate horizontal plate of bone, perforated like a sieve by a great many small holes, and thence called the **cribriform** plate (Fig. 116, *Cr.*). It is this plate (with the membranous structures which line its two faces) alone which, in this region, separates the cavity of the nose from that which contains the brain. The olfactory lobes, which are directly connected with, and form indeed a part of, the brain, enlarge at their ends, and their broad extremities rest upon the upper side of the cribriform plate, sending through it immense numbers of

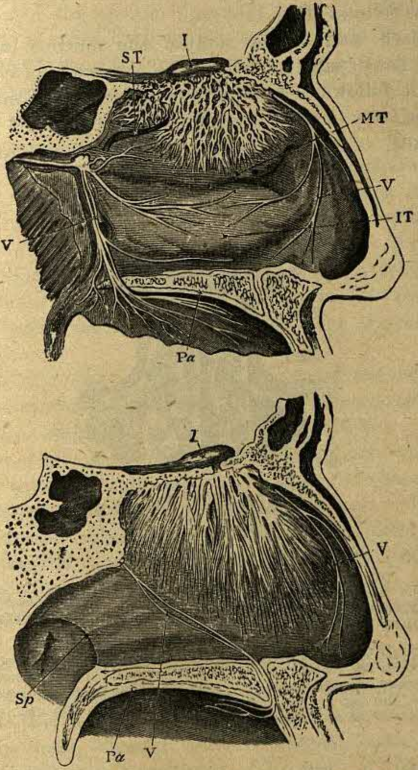

FIG. 115.—VERTICAL LONGITUDINAL SECTIONS OF THE NASAL CAVITY.

The upper figure represents the outer wall of the left nasal cavity; the lower figure the right side of the middle partition, or septum (*Sp.*) of the nose, which forms the inner wall of the right nasal cavity. *I*, the olfactory nerve and its branches; *V*, branches of the fifth nerve; *Pa.* the palate, which separates the nasal cavity from that of the mouth; *S.T*, the superior turbinal bone; *M.T*, the middle turbinal; *I.T*, the inferior turbinal. The letter *I* is placed in the cerebral cavity; and the partition on which the olfactory lobe rests, and through which the filaments of the olfactory nerves pass, is the cribriform plate.

delicate filaments, the olfactory nerves, which are distributed as follows (Fig. 115) :—

On each wall of the septum the mucous membrane forms a flat expansion, but on the side walls of each nasal cavity it follows the elevations and depressions of the inner surfaces of what are called the **upper** and **middle turbinal**, or spongy **bones.** These bones are called

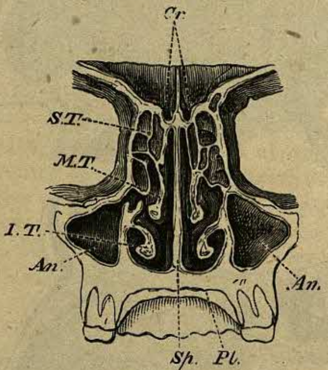

FIG. 116.—A TRANSVERSE AND VERTICAL SECTION OF THE OSSEOUS WALLS OF THE NASAL CAVITY TAKEN NEARLY THROUGH THE LETTER *I* IN THE FOREGOING FIGURE.

Cr. the cribriform plate ; *S.T*, *M.T*, the chambered superior and middle turbinal bones on which and on the septum (*Sp.*) the filaments of the olfactory nerve are distributed ; *I.T*, the inferior turbinal bone ; *Pl.* the palate ; *An.* the *antrum* or chamber which occupies the greater part of the maxillary bone and opens into the nasal cavity.

spongy because the interior of each is occupied by air cavities separated from each other by very delicate partitions only, and communicating with the nasal cavities. Hence the bones, though massive-looking, are really exceedingly light and delicate, and fully deserve the appellation of spongy (Fig. 116).

Over these upper and middle turbinal bones, and on

both sides of the septum opposite to them, the mucous membrane is specially modified, and receives the name of **olfactory mucous membrane**; and it is to this olfactory mucous membrane that the filaments of the olfactory nerve passing through the cribriform plate are distributed.

There is a third light scroll-like bone distinct from these two, and attached to the maxillary bone, which is called the **inferior** turbinal, as it lies lower than the other two, and imperfectly separates the air passages from the proper olfactory chamber (Fig. 115). It is covered by the ordinary ciliated mucous membrane of the nasal passage, and receives no filaments from the olfactory nerve.

In the non-olfactory part of the nasal mucous membrane the epithelium cells are ordinary ciliated epithelium cells (see p. 286); but in the olfactory part the cells not only lose their cilia, but become peculiarly modified. Many of them become very slender and rod-shaped, and the delicate terminations of the olfactory nerve filaments appear to end in these modified epithelial cells, which indeed are the sense-organules of the organ of smell. The olfactory mucous membrane, with the filaments of the olfactory nerve ending in it, thus constitutes the essential part of the organ.

The cells of the olfactory mucous membrane are of two kinds, and somewhat similar to those composing a taste-bud; but their arrangement is different. Thus one kind of cell is long, slender and rod-shaped, with a large nucleus towards its inner end. The cells of the second kind are also thin and rod-like at their inner ends, but beyond the nucleus, the outer end is wide and columnar. The cells of the first kind, which are the most numerous, are supposed to be those which are specially concerned in giving rise to the sensations of smell. The olfactory mucous membrane is made up of a mass of these two kinds of cell, placed side by side and intermixed. (Fig. 117.)

The accessory part of the organ of smell may be described as follows :—

From the arrangements which have been described, it is clear that, under ordinary circumstances, the gentle inspiratory and expiratory currents will flow along the comparatively wide, direct passages afforded by so much of the nasal chamber as lies below the middle turbinal; and that they will hardly move the air enclosed in the narrow interspace between the septum and the upper and middle spongy bones, which is the proper olfactory chamber.

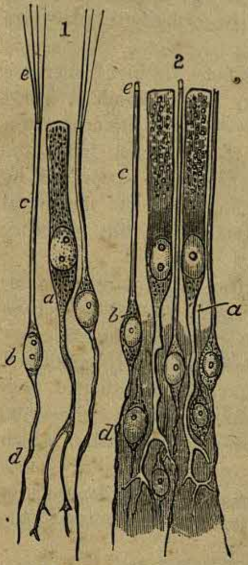

FIG. 117.—CELLS OF OLFACTORY EPITHELIUM. (MAX SCHULTZE.)

1, From a frog; 2, from man.

a, columnar epithelial cell; *b*, olfactory rod-cell; *c*, outer limb, *d*, inner limb of olfactory cell, the former being prolonged at *e* into fine hairs, the latter being continuous with a nerve filament from the olfactory nerve.

If the air currents are laden with particles of odorous matter, these can only reach the olfactory membrane by diffusing themselves into this narrow interspace; and, if there be but few of these particles, they will run the risk of not reaching the olfactory mucous membrane at all, unless the air in contact with it be exchanged for some of the odoriferous air. Hence it is that, when we wish to perceive a faint odour more distinctly, we "sniff" or snuff up the air. Each sniff is a sudden inspiration, the effect of which must reach the air in the olfactory chamber at the same time as, or even before, it affects that at the

nostrils; and thus must tend to draw a little air out of that chamber from behind. At the same time, or immediately afterwards, the air sucked in at the nostrils entering with a sudden vertical rush, part of it must tend to flow directly into the olfactory chamber, and replace that thus drawn out.

The loss of smell which takes place in the course of a severe cold may, in part, be due to the swollen state of the mucous membrane which covers the inferior turbinal bones, impeding the passage of odoriferous air to the olfactory chamber.

Very little is known of the physiology of smell, and smells have not so far been classified except as agreeable or the reverse; but recent observations seem to show that a much more detailed classification is possible, Everyday experience shows that the sense is extremely delicate, the most minute amount of odoriferous matter, such as musk, serving to excite it.

9. The Ear and the Sense of Hearing.—The ear, or organ of the sense of hearing, is very much more complex than either of the sensory organs yet described; and in it both the essential and the accessory parts are much more highly developed.

In our discussion of cutaneous sensation we saw that the skin could not be regarded as a single sense organ but that it could appreciate sensations of very different characters for which there were different types of sense organs. The same is true of the ear. It has two quite different functions, one of which is to hear sounds, the other is to acquaint the mind with the position, or alterations of the position, in which the head is placed. These different functions are located in two different parts of the ear, which, taken together, are called the inner ear. The inner ear is situated in the skull at some distance from the surface; between it and the outer, or visible portion of the ear, is the middle ear.

(i) **The External Ear.**—The outer extremity of the

external meatus is surrounded by the **concha** or external ear (*Co.* Fig. 118), a broad, peculiarly-shaped, and for the most part cartilaginous plate, the general plane of which is at right angles with that of the axis of the auditory opening. The concha can be moved by most animals and by some human beings in various directions

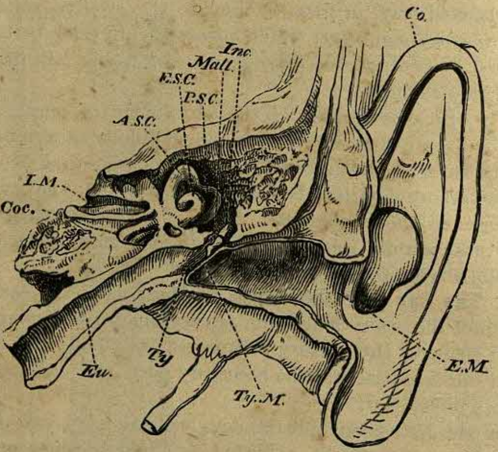

FIG. 118.—TRANSVERSE SECTION THROUGH THE SIDE WALLS OF THE SKULL TO SHOW THE PARTS OF EAR.

Co. Concha or external ear; *E.M*, external auditory meatus; *Ty.M*, tympanic membrane; *Inc. Mall*, incus and malleus; *A.S.C*, *P.S.C*, *E.S.C*, anterior, posterior, and external semicircular canals; *Coc.* cochlea; *Eu.* Eustachian tube; *I.M*, internal auditory meatus, through which the auditory nerve passes to the organ of hearing.

by means of muscles, which pass to it from the side of the head.

(ii) **The Middle Ear.**—The outer wall of the internal ear is still far away from the exterior of the skull. Between it and the visible opening of the ear, in fact, are placed in a straight line, first, the drum of the ear, or

tympanum; secondly, the long external passage, or meatus (Fig. 118).

The drum of the ear and the external meatus, which together constitute the middle ear, would form one cavity were it not that a delicate membrane, the tympanic membrane (*Ty.M*, Figs. 118 and 119), is tightly stretched in an

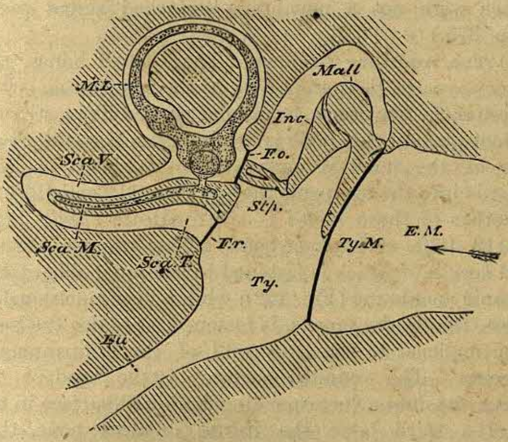

FIG. 119.—A DIAGRAM ILLUSTRATIVE OF THE RELATIVE POSITIONS OF THE VARIOUS PARTS OF THE EAR.

E.M, external auditory meatus; *Ty.M*, tympanic membrane; *Ty.* tympanum; *Mall.* malleus; *Inc.* incus; *Stp.* stapes; *F.o*, fenestra ovalis; *F.r*, fenestra rotunda; *Eu.* Eustachian tube; *M.L*, membranous labyrinth, only one semicircular canal with its ampulla being represented: *Sca.V*, *Sca.T*, *Sca.M*, the scalæ of the cochlea, which is supposed to be unrolled.

oblique direction across the passage, so as to divide the comparatively small cavity of the drum from the meatus.

The membrane of the tympanum thus prevents any communication, by means of the meatus, between the drum and the external air, but such a communication is provided, though in a roundabout way, by the Eustachian

tube (*Eu.* Figs. 118 and 119), which leads directly from the fore part of the drum inwards to the roof of the pharynx, where it opens. (See also Fig. 69.)

Two other orifices exist in the bony wall of the middle ear, they are called the *fenestra ovalis* (Fig. 119, F.o.) and the *fenestra rotunda* (F.r.) respectively. Through these the middle and inner ears would communicate with one another were not a membrane stretched across each. (See p. 375.)

(iii) **The Auditory Ossicles.**—Three small bones, the auditory ossicles, lie in the cavity of the tympanum. One of these is the **stapes**, a small bone shaped like a stirrup. The foot-plate of this bone is firmly fastened to the membrane of the fenestra ovalis, while its hoop projects outwards into the tympanic cavity (Figs. 119 and 122).

Another of these bones is the **malleus** (*Mall.* Figs. 118, 119, 122), or hammer-bone, a long process, the so-called *handle*, of which is fastened to the inner side of the tympanic membrane (Fig. 122); while a very much smaller process, the *slender process*, is fastened, as is also the body of the malleus, to the bony wall of the tympanum by ligaments. The rounded surface of the head of the malleus fits into a corresponding hollowed surface in the end of a third bone, the **incus** or anvil bone, thus forming a joint of a somewhat peculiar character. The incus has two processes; of these one, the shorter, is horizontal, and rests upon a support afforded to it by the walls of the tympanum; while the other, the longer, is vertical, descends almost parallel with the long process of the malleus, and articulates[1] with the stapes (Figs. 119 and 122).

The three bones thus form a movable chain between the fenestra ovalis and the tympanic membrane. The malleus and incus are, by the peculiar joint spoken of

[1] A minute bone, the *os orbiculare*, intervenes between the end of the process of the incus and the stapes, so that the stapes is in reality articulated with the os orbiculare, which in turn is fastened to the process of the incus. For simplicity's sake, mention of this is omitted above.

above, articulated together in such a manner that they may practically be considered as forming one bone which turns upon a horizontal axis. This axis passes through the horizontal process of the incus and the slender process of the malleus, and its ends rest in the walls of the tympanum. Its general direction is represented by the line *a b* in Fig. 122, or by a line perpendicular to the plane of the paper, passing through the head of the malleus in Fig. 119.

The two bones may be roughly compared to two spokes of a wheel, of which the axle is represented by the axis just described; it should be added, however, that one spoke, the incus, is shorter than the other, and that the movement of the two spokes is limited to a very small arc of a circle.

When the membrane of the drum, thrown into vibration by some sound, moves inwards and outwards in its vibrations, it necessarily carries with it, in each inward and outward movement, the handle of the malleus which is attached to it. But with each inward and outward movement of the handle of the malleus, the long process of the incus also moves inward and outward, carrying with it the stapes which is attached to its end. Hence each vibration, each inward thrust, and each outward or backward return of the membrane of the drum, produces by means of the chain of ossicles a corresponding vibration of the membrane of the fenestra ovalis to which the stapes is attached.

(iv) **The Muscles of the Tympanum.**—The characters of the vibration of a membrane, and the readiness with which it takes up or responds to, aërial vibrations reaching it, are largely modified by its degree of tension; the membrane acts differently when it is tightly stretched from what it does when it is loose. Now, within the cavity of the tympanum are two small, but relatively strong muscles. One, called the **stapedius**, passes from the floor of the tympanum to the foot of the stapes and the orbicular bone, the other, the **tensor tympani**, from

the front wall of the drum to the malleus. Each of the muscles when it contracts tightens the membrane to which it is thus indirectly attached, the tensor tympani, the membrane of the drum, and the stapedius, the membrane of the fenestra ovalis. The effect of thus tightening the membrane is probably to restrict the vibrations of the membrane, at least as far as concerns grave, or low-pitched sounds, but the complete action of these muscles is too intricate to be dwelt on here.

(v) **The Inner Ear** consists, substantially, of a very peculiarly-formed membranous bag. This bag, when the ear first begins to be formed, is a simple round sac, but it subsequently takes on a very complicated form, and becomes divided into several parts, which receive special names. It is lodged in a cavity of correspondingly intricate shape, hollowed out of a solid mass of bone (called from its hardness *petrosal*), which forms part of the temporal bone, and lies at the base of the skull. The sac, however, does not completely fill the cavity, so that a space is left between the bony walls and the contained sac. This space, otherwise continuous all round the sac, is interrupted at certain places only where the membranous sac is attached to the bony walls, and contains a fluid provided by the lymphatics of the neighbourhood, and called **perilymph**.

The membranous sac, the walls of which consist chiefly of connective tissue, is lined by an epithelium, and contains a fluid of its own called **endolymph**. The perilymph, it will be understood, is quite distinct from the endolymph, the two fluids being separated by the walls of the membranous sac.

Over a great part of the interior of the membranous sac the epithelium is simple in character, but at certain places to be presently described it assumes special features.

So much is true of the sac as a whole, but the different portions of it have very different functions. The general shape of the sac is shown diagrammatically in Fig. 124.

It is divided roughly into two compartments, the utricle and the saccule; with the former is connected a system of tubes known as the semicircular canals, with the latter is connected a single tube which is coiled in the shape of a helix. This tube is the *canalis cochlearis*, and with the bony cavity in which it is enclosed, forms the cochlea, the essential organ of hearing.

(vi) **The Cochlea.**—Connected with the saccule by a narrow canal is an extension of the original membranous sac, in the form of a long tube closed at the end (Fig. 124, *Coch.*). This cochlear tube is lined with epithelium, contains endolymph, and is lodged in a bony cavity filled with perilymph. The canalis cochlearis is much smaller in section than the bony cavity in which it lies. The amount of perilymph surrounding it is therefore considerable. In the cochlea the contour of the cochlear tube is, along its whole length, totally different from that of the containing cavity; for, in transverse section, while the contour of the containing cavity is almost circular, that of the cochlear tube itself is nearly triangular. The cochlear tube in fact is, in shape, what is often called triangular (as when we speak of a triangular file), but should be called *trihedral*; that is to say it has three sides or faces (and three edges); one of the sides is however not flat but convex, *i.e.*, bulges somewhat outwards.

The cochlear tube, or canalis cochlearis, closely adheres to the bony wall, along the whole length of the tube, in two regions, namely, over the whole of that face of the trihedral tube which has just been described as being convex, and at the edge opposite. Take a round ruler, make a paper case which just fits it, and close the case at one end. Then pare down the ruler on two sides until it has two flat faces meeting at an edge, and slide it into the case, so that it does not quite reach the closed end. The ruler, if it were hollow, would represent the cochlear tube; and it will be observed that it divides the cavity of the case into two passages, which are quite distinct from

each other, except at the end of the case to which the ruler does not reach. In a similar way, the cochlear tube, containing endolymph, divides the cavity containing perilymph, in which it lies, into two passages, called **scalæ**, which are seen in section (Fig. 120) to be placed one above and the other below the triangular cavity of the cochlear tube itself, and which communicate with each other at the far end of the cochlear tube, but not elsewhere.

In one point, however, the comparison with the ruler and its case is not exact. The cochlear tube is not nearly so wide as the containing cavity; and the sharp edge opposite the convex adherent face would not be in direct connexion with the bony walls, were it not for a bony ledge which, projecting from the bony walls towards the thin edge of the cochlear tube, is united to it by membrane and thus forms a partition or **septum**, which separates the two scalæ in the region where the cochlear tube itself would otherwise leave a communication between them.

As has been already stated the cochlear tube is not straight or even simply curved, but is twisted up on itself into a spiral of two and a half turns. In these twists it is accompanied by the cavities above and below it, and also by the septum spoken of above, which thus takes a spiral course, and is spoken of as the **lamina spiralis** (Figs. 120, *L.S*, 121, *l.s*). The whole arrangement somewhat resembles the shell of a snail; hence the name. All along the spiral the edge of the cochlear tube attached to the lamina spiralis is directed inwards and the convex face outwards; so that when a section is made through the axis of the spiral a succession of rounded spaces are cut through, each space exhibiting, above and below, the somewhat half-moon-shaped section of a *scala*, the two scalæ being separated on the outer side, by the cochlear tube, and, on the inner, by the lamina spiralis (Fig. 120).

The triangular cavity which, as we have seen, contains

endolymph, and is continuous with the saccule, is called the **canalis cochlearis.** The upper of the two cavities containing perilymph, when traced down to the bottom of the spiral, is found to be continuous with the cavity containing perilymph which surrounds the vestibule (*i.e.*, the utricle and saccule); hence it is called the **scala vestibuli.** The lower cavity, when similarly traced to the bottom of the spiral, ends at the **fenestra rotunda,** which is closed by a membrane. Since this lower cavity is only separated from the middle ear or tympanum by

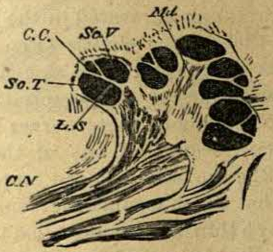

FIG. 120.—A SECTION THROUGH THE AXIS OF THE COCHLEA, MAGNIFIED THREE DIAMETERS.

C.C, canalis cochlearis, or cochlear tube; *Sc.V*, scala vestibuli; *Sc.T*, scala tympani; *L.S*, lamina spiralis; *Md.* bony axis, or modiolus, round which the scalæ are wound; *C.N*, cochlear nerve.

the membrane covering the fenestra rotunda, it is called the **scala tympani.** Thus the scala vestibuli and scala tympani begin at different points, and are separated along their whole course by the cochlear tube and the lamina spiralis except at the very tip of the spiral, where these latter end; here the two scalæ are prolonged beyond the cochlear tube and join together, forming a common space, as seen at the top of Fig. 120.

The vibrations of sound are brought, as we shall see, to the perilymph chamber of the vestibule, whence they spread on the other into the scala vestibuli. Passing upwards, in the spiral along the scala vestibuli, they enter at

the summit the scala tympani, along which they descend, and are eventually lost at the fenestra rotunda in which that scala ends.

(vii) **The Organ of Corti.**—But besides this peculiar arrangement of the perilymph chamber, there are other and still more important differences between the cochlea and the labyrinth.

The auditory nerve is, as we have seen, distributed to certain parts only of the membranous labyrinth, namely, to the crests of the ampullæ and to the patches on the utricle and the saccule; but, in the case of the cochlea, fibres, running in canals excavated in the bony core of the spiral, and in the lamina spiralis (Fig. 121, *A.N*) run to and end in the canalis cochlearis along its whole length, from the bottom to the top of the spiral, Fig. 124, *Coch.* And the mode of ending of these nerves is very peculiar.

If we examine a section of one of the spirals of the cochlea (Fig. 121), we see that the upper side of the cochlear tube (that which separates it from the scala vestibuli) is formed by a thin membrane (called the **membrane of Reissner**, Fig. 121, *m.R*) lined internally by simple epithelium. The outer convex side of the cochlear tube, that side by which it is firmly attached to the bony wall, is also lined internally by simple epithelium. Neither here nor in the membrane of Reissner do any fibres of the auditory nerve end. But the remaining side of the tube, that which looks towards the scala tympani, possesses on its inner face, along the whole length of the tube, from the bottom to the top of the spiral, a very remarkable and strangely modified epithelium; and, along the whole length of the tube, fibres of the auditory nerve pass into and end among the cells of this epithelium, which is spoken of as the **organ of Corti.** (Fig. 121, *O.C.*)

The membrane which separates the cavity of the cochlear tube from the scala tympani, and on which the organ of Corti is placed, is of a peculiar character, speci-

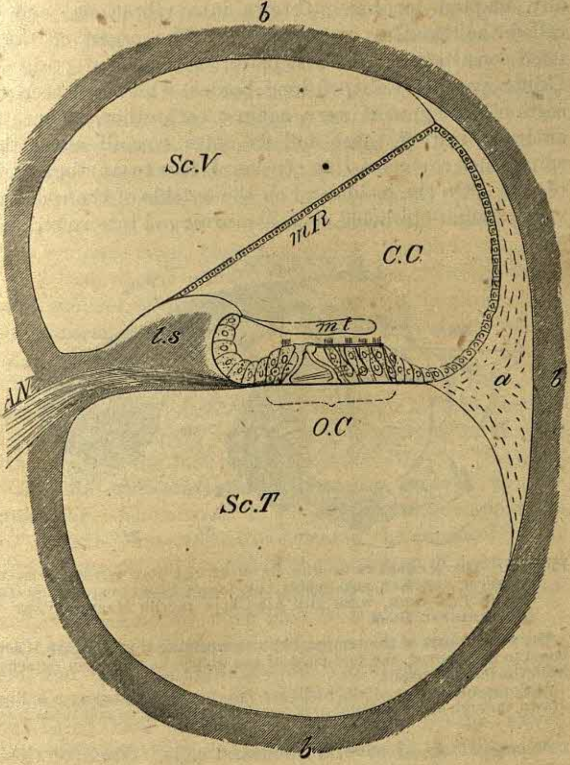

FIG. 121.—SECTION OF COIL OF COCHLEA.

Sc.V, scala vestibuli; *Sc.T*, scala tympani; *C.C*, canalis cochlearis, or scala media; *O.C*, organ of Corti; *m.R*, membrane of Reissner, *m.t*, membrana tectoria (a gelatinous membrane overlying the organ of Corti, and supposed to act as a damper). *A.N*, fibres of the auditory nerve running in *l.s*, the lamina spiralis, and ending in the organ of Corti; *a*, connective tissue cushion to which the basilar membrane is attached on the outside; *b*, bony walls.

The figure has, for simplicity's sake, been made somewhat diagrammatic. The lamina spiralis has been drawn too short; the proportions of the lamina spiralis and the scalæ are more exactly rendered in Fig. 120.

ally adapted for being thrown into vibrations, and is called the **basilar membrane**. The organ of Corti itself consists of, in the first place, the so-called **rods of Corti**, peculiarly shaped long bodies, which are seen in section leaning, as it were, against each other. There is an inner row of these and an outer row all along the spiral, each row consisting of several (four to six) thousands of rods. On the inside and on the outside of the rods are very peculiar epithelial cells, also arranged into rows, each

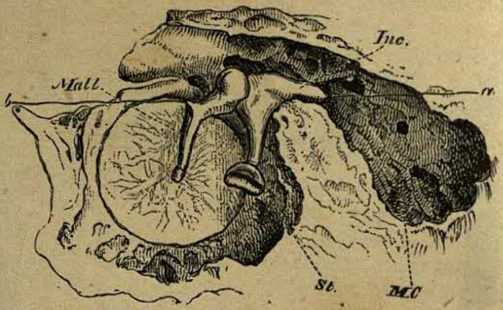

FIG. 122. THE MEMBRANE OF THE DRUM OF THE EAR WITH THE SMALL BONES OF THE EAR SEEN FROM THE INNER SIDE; AND THE WALLS OF THE TYMPANUM, WITH THE AIR-CELLS IN THE MASTOID PART OF THE TEMPORAL BONE.

The petrous part of the temporal bone containing the labyrinth is supposed to be removed, the foot-plate of the stapes having been detached from the fenestra ovalis.

M.C, mastoid cells; *Mall.* malleus; *Inc.* incus; *St.* stapes; *a b*, lines drawn through the horizontal axis on which the malleus and incus turn.

row consisting of several thousand cells. Each of these cells bears short hairs on its free surface, hence they are called hair-cells, inner and outer; and the auditory nerves passing through the lamina spiralis, reach the cochlear tube along the whole length of the spiral and end in filaments which are lost in the organ of Corti, but are probably connected with the hair-cells.

(viii) **The Bony Labyrinth.**—The essential part of the organ of hearing, the canalis cochlearis, as well as the

other structures developed from the original sac, is lodged in chambers of the petrous part of the temporal bone.

In the fresh state, this collection of chambers in the petrous bone is perfectly closed; but, in the dry skull, there are (as we have seen, p. 370) two wide openings, termed **fenestræ**, or windows, on its outer wall; *i.e.*, on the side nearest the outside of the skull. Of these fenestræ, one, termed **ovalis** (the oval window), is situated in the wall of the vestibular cavity; the other, **rotunda** (the round window), behind and below this, is, as we have seen, the open end of the *scala tympani* at the base of the spiral of the cochlea. In the fresh state, each of these windows or fenestræ is closed by a fibrous membrane, continuous with the periosteum of the bone.

The *fenestra rotunda* is closed by membrane only; but fastened to the centre of the membrane of the *fenestra ovalis*, so as to leave only a narrow margin, is an oval plate of bone, the foot of the stapes (p. 370).

(ix) **The Transmission of Sound Waves to the Inner Ear.**—The manner in which the complex apparatus now described intermediates between the physical agent, which is the primary cause of the sensation of sound, and the nervous expansion, the affection of which alone can excite that sensation, must next be considered.

All bodies which produce sound are in a state of vibration, and they communicate the vibrations of their own substance to the air with which they are in contact and thus throw that air into waves, just as a stick waved backwards and forwards in water throws the water into waves.

The aërial waves, produced by the vibrations of sonorous bodies, in part enter the external auditory passage, and in part strike upon the concha of the external ear and the outer surface of the head. It may be that some of the latter impulses are transmitted through the solid structure of the skull to the organ of hearing; but before they

reach it they must, under ordinary circumstances, have become so scanty and weak, that they may be left out of consideration.

The aërial waves which enter the meatus all impinge upon the membrane of the drum and set it vibrating, stretched membranes, especially such as have the form and characters of the tympanic membrane, taking up vibrations from the air with great readiness.

The vibrations thus set up in the membrane of the tympanum are communicated, in part, to the air contained in the drum of the ear, and, in part, to the malleus, and thence to the other auditory ossicles.

The vibrations communicated to the air of the drum impinge upon the inner wall of the tympanum, on the greater part of which, from its density, they can produce very little effect. Where this wall is formed by the membrane of the *fenestra rotunda* the communication of motion must necessarily be greater. All these vibrations. however, may probably be neglected.

The vibrations which are communicated to the malleus and the chain of ossicles may be of two kinds : vibrations of the particles of the bones, and vibrations of the bones as a whole. If a beam of wood, freely suspended, be very gently scratched with a pin, its particles will be thrown into a state of vibration, as will be evidenced by the sound given out, but the beam itself will not be visibly moved. Again, if a strong wind blow against the beam, it will swing bodily, without any vibrations of its particles among themselves. On the other hand, if the beam be sharply struck with a hammer, it will not only give out a sound, showing that its particles are vibrating, but it will also swing, from the impulse given to its whole mass.

Under the last-mentioned circumstances, a blind man standing near the beam would be conscious of nothing but the sound, the product of molecular vibration, or invisible oscillation of the particles of the beam ; while

a deaf man in the same position would be aware of nothing but the visible oscillation of the beam as a whole.

Thus, to return to the chain of auditory ossicles, while it may be supposed that, when the membrane of the drum vibrates, these may be set vibrating both as a whole and in their particles, the question arises whether it is the large vibrations, or the minute ones, which make themselves obvious to the auditory nerve which is in the position of our deaf, or blind, man.

The evidence is distinctly in favour of the conclusion, that it is the vibrations of the bones, as a whole, which are the chief agents in transmitting the impulses of the aërial waves.

For, in the first place, the disposition of the bones and the mode of their articulation are very much against the transmission of molecular vibrations through their substance, but, on the other hand, are extremely favourable to their vibration *en masse*. The long processes of the malleus and incus swing, like a pendulum, upon the axis furnished by the short processes of these bones; while the mode of connection of the incus with the stapes, and of the latter with the membrane of the fenestra ovalis, allows the foot-plate of that bone free play, inwards and outwards. In the second place, the total length of the chain of ossicles is very small compared with the length of the waves of audible sounds, and physical considerations teach us that in a like thin rod, similarly capable of swinging *en masse*, the minute molecular vibrations would be inappreciable. Thirdly, direct experiments, such as attaching to the stapes of a dissected ear a light style, the movements of which are recorded on a travelling smoked glass plate or in some other way, show that the chain of ossicles does actually vibrate as a whole, and at the same rate as the membrane of the drum, when aërial vibrations strike upon the latter.

Thus, there is reason to believe that when the tympanic membrane is set vibrating, it causes the process of the malleus, which is fixed to it, to swing at the same rate; the head of the malleus consequently turns through a small arc on its pivot, the slender process. But, as stated on p. 371, the turning of the head of the malleus involves the simultaneous turning of the head of the incus upon its pivot, the short process. In consequence the long process of the incus also swings at the same rate. The length of the long process of the incus, measured from the axis, on which the two bones turn, is less than that of the handle of the malleus; hence the end of it moves through a smaller space. The arc through which it moves has been estimated as being equal to about two-thirds of that described by the handle of the malleus. The extent of the push is thereby somewhat diminished, but the force of the push is proportionately increased; in so confined a space this change is advantageous. The long process of the incus, however, is so fixed to the stapes, and the stapes so attached to the membrane of the fenestra ovalis, that the incus cannot vibrate without throwing into vibrations, to a corresponding extent and at the same rate, the membrane of the fenestra ovalis. But every vibration, every pull and push, imparts a corresponding set of shakes to the perilymph, which fills the vestibule, the scala vestibuli and the scala tympani. These shakes are communicated to the endolymph in the canalis cochlearis, and, in some way, stimulate the delicate endings of the cochlear division of the auditory nerve. Probably the vibrations of the basilar membrane play an important part.

(x) **The Conversion of Sonorous Vibrations into Sensations of Sound.**—We do not at present know what kind of changes the vibrations of the endolymph give rise to in the cochlea; nor do we at present know the exact way in which the changes thus set up are able to excite the terminal filaments of the auditory nerve. But

there can be no doubt of the fact that the elaborate apparatus of the cochlea is able to translate, so to speak, the sonorous vibrations which reach it into stimulations of nerve fibres, the molecular changes of which are transmitted along the auditory nerve as nervous impulses. Passing along the auditory nerve, these molecular changes, these nervous impulses, reach certain parts of the brain, situated in the cortex of the temporo-sphenoidal lobe, below the fissure of Sylvius (see Lesson XI.), and there in turn set up those molecular disturbances of nervous matter which form the immediate cause of the states of feeling called "sounds." Thus the auditory nerve may be said, and a similar statement may be made in the case of the other nerves of special sensations, to be provided with two "end-organs." There is the **peripheral end-organ** (the apparatus of the cochlea and labyrinth), by which the physical agent is enabled to excite the sensory nerve-fibres; and there is the **central end-organ**, in the brain, in which the nervous impulses of the sensory nerve excite the special state of feeling which we call the special sensation. The central end-organ of hearing is often spoken of as the auditory sensorium.

Between the emission of sound from a body and its appreciation by the hearer there is a series of events of different kinds. There are the vibrations started by the sounding body, and passing through the air, the tympanum, the perilymph, and the endolymph; these are all of one order. Then there are the changes in the peripheral end-organ, in the apparatus of the cochlea and labyrinth; these are of another order. Then follow the molecular disturbances travelling along the auditory nerve; these are of still another order. Lastly, there are the changes in the central end-organ, in the brain; these, though resembling the preceding in so far as they are changes of nervous matter, are yet of still another order, and probably comprise in themselves a whole series

of events, the consequence of the last of which is the sensation of sound.

Every sound consists, as we have seen, of vibrations. Sometimes the vibrations are repeated with great regularity; and sounds, in which the regular recurrence of the same vibrations is conspicuous, are called "musical sounds." Sometimes no regular repetition of vibrations can be recognised; the sound consists of vibrations, few of which are like each other, and which fall irregularly on the ear; such sounds are called "noises."

When we listen to musical sounds, each set of regularly repeated vibrations generates in the central end-organ a particular kind of sensation which we call a *tone*; and the simultaneous or successive production of different tone-sensations gives rise in us to the feelings which we speak of as those of harmony or melody.

When we listen to a noise the vibrations generate sensations which are of a certain intensity, according to which we call the noise slight or great, low or loud, and which also have certain characters by which we recognise the kind of noise; but the sensations have not the qualities of tone-sensations, and do not give rise to feelings of melody or harmony.

A pure musical sound consists of a series of vibrations repeated with exact regularity, the number of vibrations occurring in a given time, *e.g.* in a second, determining what is called the pitch of the "note." But ordinary musical sounds are, for the most part, not simple, consisting of one set of vibrations, but compound, consisting of several sets of vibrations occurring together; in these musicians distinguish one set, called the **fundamental tone**, and other sets, varying in intensity or loudness, called **overtones**.

A tuning-fork, when set vibrating, vibrates with a given rapidity; and the note given out is determined by the rapidity of the vibration, by the number of vibrations repeated, for instance, in a second; hence every tuning-fork

has its own proper note. Now, a tuning-fork will be set vibrating if its own particular note be sounded in its neighbourhood, but not if other notes be sounded. Hence, when a pure musical note is sounded close to a number of tuning-forks of different pitch, only that tuning-fork the pitch of which is the same as that of the note sounded is set vibrating; the others remain motionless. When an ordinary musical sound, such as a note sung by the human voice, is produced among such a group of tuning-forks, several are set vibrating; one of these corresponds to the fundamental tone, and the others to the various overtones of the sound. Similarly, if the top of a piano be lifted up or removed, and any one sings into the wires with sufficient loudness, a note, such as the tenor C, a number of the wires will be set vibrating, one corresponding to the fundamental tone, and the others to the overtones.

If we were to imagine an immense number of tuning-forks, each vibrating at different periods, so arranged that each fork, when vibrating, in some way or other stimulated or excited a minute delicate nerve-filament attached to it, it is obvious that a musical sound uttered near these tuning-forks would set a certain number of them into vibration, some more forcibly than others, and that in consequence a certain number, and a certain number only, of the delicate nerve-filaments would be excited, and that to various degrees; and thus a particular series of nervous impulses, the counterpart as it were of the musical sound with its fundamental tone and overtones, would be transmitted along the nerve filaments to the brain.

And it is suggested that the basilar membrane of the cochlea, consisting as it does of thousands of fibres stretching across from the inside to the outside (from left to right in Fig. 121), with its thousands of epithelial cells and rods of Corti lying upon it, represents, as it were, an assemblage of thousands of tuning-forks, of various rates of vibration, with a separate nerve filament attached to each. So that, when a number of vibrations of different

periods, such as constitutes an ordinary musical sound, are transmitted by the tympanum to the cochlea, these as they sweep along the canalis cochlearis throw into sympathetic movement those parts, and those parts only, of the basilar membrane with their overlying epithelium, whose periods of vibration correspond to their own vibrations, and thus excite certain nerve filaments, and these only. It is this excitement of a group of nerve filaments, some more intensely than others, which, reaching the brain, give rise to the sensation which we associate with the particular musical sound.

It must be distinctly understood that the picture which has just been drawn only illustrates one way in which the cochlear mechanism *might* translate waves in the perilymph into nervous impulses. There is no suggestion that this indicates what actually takes place or even that it is nearer the truth than any of several other suggestions which have been made. It is possible for instance that each wave in the perilymph causes the whole basilar membrane to vibrate like the plate of a telephone or itself to fall into waves which traverse its whole length, in either case we can conceive that the hair cells could appreciate such a condition.

Little as we know of the cochlear mechanism, we know still less about the nature of the auditory sensorium or central end-organ of the auditory nerve; but it may be conceived that each filament of the cochlear nerve is connected with a particular portion of the nervous matter of the central end-organ, in such a way that the molecular movements of one of these particular portions of nervous matter, brought about by a molecular disturbance reaching it through its appropriate filament, produces a psychical effect of one kind only, more or less intense it may be, but still always of one kind. If this be so, each cochlear fibre or filament may be considered as being provided with two end-organs: one, peripheral, in the organ of Corti, capable of being set in motion by

vibrations of one quality only ; the other, central, in the brain, capable of producing a psychical effect of one quality only. It does not follow, however, that we are distinctly and separately conscious of the nervous disturbance in each central end-organ, it does not follow that we have as many distinct and separate kinds of conscious sensation as there are peripheral and central end-organs, though how many such distinct kinds of sensation we may have we do not know. Just as the peripheral mechanism sifts out the several vibrations of which a musical sound is composed, and transmits them separately, so, by a reverse operation, the central mechanism probably pieces together the nervous disturbances of a number of central end-organs, and thus produces a sensation whose characters are determined by a combination of the nervous disturbances taking place in each end-organ.

Some such a view is indeed exceedingly probable ; but it must be remembered that we do not at present at all understand the exact mechanism by which each particular vibration excites its corresponding nerve filament. The nerve filaments appear to end in the epithelial cells bearing short hairs, which lie on each side of the rods of Corti ; and we may therefore conclude that these "hair-cells" have some share in producing the effect. But the whole matter is at present very obscure ; the functions of the rods of Corti are particularly difficult to understand ; for these do not seem in any way connected with the nerve filaments, and their movements can only affect the latter by influencing in some way the hair-cells.

The fibres of the cochlear nerve, or their endings in the brain itself, may be excited by internal causes, such as the varying pressure of the blood and the like ; and in some persons such internal influences do give rise to veritable musical spectra, sometimes of a very intense character. But, for the appreciation of music produced external to us, we depend upon the organ of Corti being

in some way or other affected by the vibrations of the fluids in the cochlea.

(xii) **Localisation of Sound.**—The apparatus of the ear which we have described, provides us simply with auditory sensations; enables us to appreciate high notes and low notes, to discriminate between musical sounds and noises. Experience then enables us to base upon these sensations certain conclusions as to the nature of the source which is giving rise to each sound. The conclusions we thus arrive at are usually more or less accurate. But sounds may be coming to us in different directions and from different distances, and when we endeavour to form some estimate of either the one or the other of these possible differences we find our means of doing so are very imperfect. As to our estimate of the distance from which a sound is coming, we are guided chiefly by its varying intensity coupled with previous experience and a knowledge of the laws which connect varying intensity with the different distances of the source. For the discrimination of the direction from which a sound is coming, we have to rely almost entirely on the different effect the sound produces on each of our two ears, according as it falls more directly into one of them than into the other. Thus when we are endeavouring to localise a source of sound, we usually turn the head into various positions until we find one position in which the sound is loudest as it falls into one ear, and then we assume that the sound is coming along a line directed straight into that ear. In animals with large and movable external ears, the movement of the ear to a great extent takes the place of the movement of the head; this may be readily observed in an animal such as the horse.

Anything which interferes with the ordinary laws of transference of sound causes us to form a wrong judgment as to the distance of the source, as in the case of listening to speech through a telephone or in a phonograph. Similarly, it is difficult to estimate the distance of the

source of a sound heard through a snow storm. Again, in ventriloquism our judgment is upset, not only as regards the nature of the source of sound, but also of its distance and direction, by carefully planned simulation and suggestion.

(xiii) **The Functions of the Tympanic Muscles and Eustachian Tube.**—It has already been explained that the *stapedius* and *tensor tympani* muscles are competent to tighten the membrane of the fenestra ovalis and that of the tympanum, and it is probable that they come into action when the sonorous impulses are too violent, and would produce too extensive vibrations of these membranes. They may therefore be of use in moderating the effect of intense sound, in much the same way that, as we shall find, the contraction of the circular fibres of the iris tends to moderate the effect of intense light in the eye; they may, however, have other purposes.

The function of the Eustachian tube is, probably, to keep the air in the tympanum, or on the inner side of the tympanic membrane, of about the same tension as that on the outer side, which could not always be the case if the tympanum were a closed cavity. The unpleasant sensation often experienced, as of a "tightness" in the ear, when diving under water, is due to the compression of the air in the tympanic cavity under the increased external pressure. It may be largely removed by merely performing the movements of swallowing. By these movements the end of the Eustachian tube which opens into the pharynx is opened and the pressure on the two sides of the tympanum is equalised.

10. Sensations governing co-ordination and equilibrium.—The sense of sight is associated with the eye and with no other sense organ, that of hearing with the ear and so forth; in each case we are fully conscious of our use of these faculties. But there is another sense of which we are as a rule unconscious, this is the sense of co-ordination; when this sense fails us however we become

amply conscious of the failure, which we signify by the word giddiness. This word is not always used in quite the same sense. It will be worth while to inquire more particularly what we mean by it.

To take an instance, many persons, if they have to look down from a considerable height, such as the edge of a precipitous cliff, or the tower of a high building, or in some cases even a scaffold, say they feel giddy. This feeling, which it is difficult to describe, at all events involves the inability to carry out or co-ordinate ordinary movements, and would if strong enough lead to complete collapse, in which case the person would not only be unable to proceed but would actually fall. Again, if a person turns round rapidly a few times and then stops he describes himself as feeling giddy, but in this case he has a perfectly definite sensation that the room is swinging round ; at the same time if he tries to move his gait is unsteady, and if he is giddy enough he falls down.

The power of co-ordination of the muscles, which enables the body to maintain its equilibrium, is the result of sensations which come from more than one sense organ. In the first of the two instances of giddiness which have been given, the cause of giddiness was in really a failure of the sense of sight to adapt itself to unaccustomed conditions; indeed, in some persons the giddiness experienced in lofty positions is overcome by the adequate use of glasses. The sense of sight is one of those which contribute to the power of co-ordination. Sensations which come from the limbs are also factors. This is evident in the condition of persons stricken with locomotor ataxy. The gait of one suffering from this malady is extremely clumsy and unsteady, and, indeed, is only possible because he can use his vision instead of the sensations which, owing to the diseased condition of his spinal cord, fail to come from his legs. He walks by seeing a spot in front of him at a suitable distance and planting his foot upon it ; blindfolded he would at once

fall. The particular sensation from the legs, which in a normal person help in co-ordination, are to some slight extent those from the skin of the feet, but more especially are those from the joints and the muscles. These sensations from the limbs are thus the second class of sensation which contribute to the power of coordination.

But even more important than either the sensations from the eyes or from the limbs are a third set which come from a special organ which exists for the purpose of appreciating alterations in the position of the body with regard to the objects around it just as definitely as the

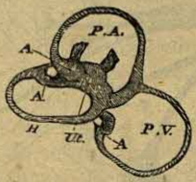

FIG. 123.—THE MEMBRANOUS LABYRINTH, TWICE THE NATURAL SIZE.

Ut. the *Utricle*, or part of the vestibular sac, into which the semicircular canals open; *A. A. A*, the ampullæ; *P.A*, anterior vertical semicircular canal; *P.V*, posterior vertical semicircular canal; *H*, horizontal semicircular canal. The saccule is not seen, as in the position in which the labyrinth is drawn the saccule lies behind the utricle. The white circles on the ampullæ of the posterior vertical, and horizontal canals indicate the cut ends of the branches of the auditory nerve ending in those ampullæ; the branch to the ampullæ of the anterior vertical canal is seen in the space embraced by the canal, as is also the branch to the utricle.

eye sees or the ear hears. This organ is the membranous labyrinth of the ear, the utricle and the semicircular canals. The giddiness which is invoked by turning rapidly and then stopping suddenly gives rise to a definite sensation because this definite organ is stimulated in just the way that it would be if the person and the room were rotating relatively to one another. In order to see that this is so we must understand the structure of the labyrinth of the ear.

(i) **The Membranous Labyrinth.**—The membranous bag, as we have said, is not simple but complicated; it consists of several parts. In the first place there is a somewhat oval sac, called the **utricle** (Fig. 123, *Ut.*) into which open three hoop-like semicircular canals. Of these two are placed vertically, one directed anteriorly, the other posteriorly, and are hence called the

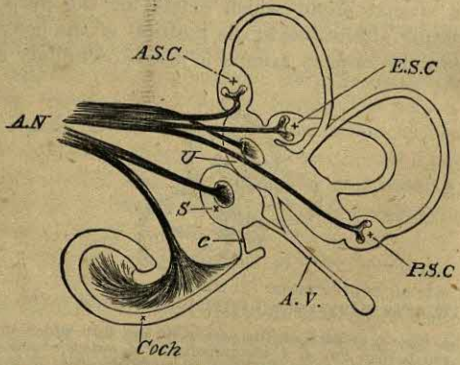

FIG. 124.

Diagram to illustrate the endings of the auditory nerve in the membranous labyrinth and cochlea. N.B. *The drawing is diagrammatic.*

A.N, auditory nerve dividing into several branches, and ending:—at *A.S.C*, in the ampulla of the anterior vertical semicircular canal: *P.S.C*, do. posterior vertical: *E.S.C*, do. external horizontal: *U*, in the utricle: *S*, in the saccule. *Coch.* the ending all along the canalis cochlearis; *A.V*, canal uniting the interior of utricle with that of saccule. *C*, canal joining the saccule to the canalis cochlearis.

anterior (*P.A*) and **posterior** (*P.V*) **vertical semicircular canals.** The third is placed horizontally and directed outwards, hence it is called the **exterior horizontal semicircular canal** (Fig. 123, *H*). It will be observed that the three canals thus lie in the three directions of space. Each of these three hoops is

dilated at one of its two ends, where it opens into the utricle, into what is called an **ampulla** (Fig. 123, *A*, *A*, *A*), the other end having no ampulla. Thus there is one ampulla to each canal. Those ends of the two vertical canals which are not dilated into ampullæ join together (Fig. 124), before they open into the utricle.

On each ampulla is a ridge or crest, called **crista acustica**, placed crosswise, and projecting into the cavity of the canal. Each crest is formed partly by an infolding and thickening of the connective tissue wall of the ampulla, and partly by a thickening of the epithelium, which here has the peculiar characters already referred to. A similar but oval patch of thickened, modified, auditory epithelium, with a thickening of the wall beneath it, is found in the utricle itself; this is called a **macula acustica.**

Attached to the utricule is a similar smaller sac (forming another division of the primitive membranous bag) called the **saccule**, on the walls of which is a similar rounded patch of modified epithelium, or *macula*. The cavity of the saccule is cut off from that of the utricle, except for a curious roundabout connection by means of a narrow canal (Fig. 124, *A.V.*).

The utricle and saccule with the three semicircular canals receive the name of the **membranous labyrinth.** It will be remembered that this membranous labyrinth, filled with endolymph, lies in an intricate cavity with bony walls called the **osseous labyrinth**, of which the part which contains the saccule and utricle is known as the **vestibule**, and that between the walls of the bony and the membranous labyrinth, which correspond largely but not wholly in form, is a space filled with perilymph.

Branches of the auditory nerve pass to this membranous labyrinth and send fibres (Fig. 124) to the three

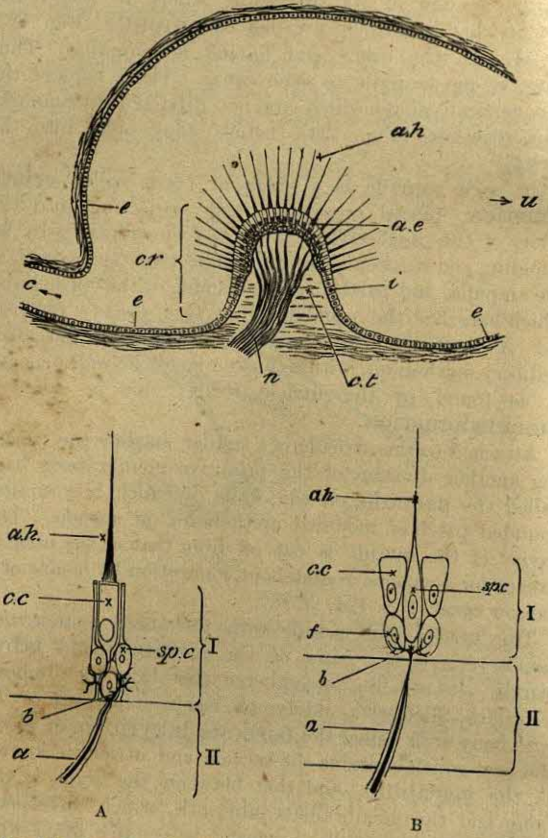

FIG. 125.—LONGITUDINAL SECTION OF AMPULLA, CUTTING THE CREST CROSSWISE (SOMEWHAT DIAGRAMMATIC).

c, one end of the ampulla forming the semicircular canal, *u*, the other end opening into the utricle; *e*, ordinary epithelium lining the greater part of the ampulla; *cr.* the crest with *a.e*, auditory epithelium; *a.h*, auditory hairs; *c.t*, connective tissue support to the auditory epithe-

crests of the three ampullæ, to the patch on the utricle, and to the patch on the saccule. In each crest and each patch the epithelium is thickened and modified, and although the crests are slightly different in structure from the patches, the general features are the same in all. Whereas over the rest of the inside of the membranous labyrinth the epithelium consists (Fig. 125, *e*) of a single layer of low, rather flat cells, in the crests and patches the cells lie several deep, and are of a peculiar form. Some are conical or cylindrical, and some are spindle-shaped, and either the one or the other, or, according to some authors, both, bear stiff hair-like filaments (Fig. 125, *a.h*, *a.h.*) projecting into the cavity of the labyrinth. These filaments, often called auditory hairs, appear at first sight to resemble cilia, but they are stiff, and unlike cilia have no active movement of their own. They are longer and more conspicuous in the crests of the ampullæ than in the patches of the utricle and saccule. The fibres of the auditory nerve may be traced through the connective tissue wall of the crest or patch into the epithelium, where they break up into a delicate network among the cells (Fig. 125, *A*, *B*, *b*); but it is not as yet exactly determined how the filaments of this network end, whether they actually join the conical cells, or the spindle cells, or merely lie in contact with them.

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lium; *n*, fibres of the auditory nerve passing into the auditory epithelium; *i*, epithelium intermediate between the auditory epithelium and the ordinary epithelium of the rest of the ampulla.

A and B, Diagrams to illustrate the character of the cells of the auditory epithelium, and the two views taken as to the relation of the auditory hairs to the cells. In both A and B, I is the auditory epithelium, II the connective tissue on which it rests, and *a*, a fibre of the auditory nerve passing through II, and dividing into fine branching filaments in I, at *b*.

In A, *c.c*, cylindrical cell bearing auditory hairs, *a.h*: each cell bears a group of fine hairs which adhere together as a long narrow cone; *sp.c*, spindle-shaped cells, not bearing hairs.

In B, *c.c*, cylindrical cells not bearing hairs, *sp.c*, spindle-shaped cells bearing the auditory hair *a.h*, and supposed to be connected with the nerve-filaments; *f*, other supporting cells.

In both A and B, the fibre, *a*, of the auditory nerve passes into the epithelium, and ends in fine branches, *b*.

Let us now revert to the relation of the semicircular canals to giddiness. If a glass containing water in which some powder has been placed be rotated, the observer will see, by looking at the powder, that whilst the glass rotates the water does not. This is so at first at all events, but if the rotation be maintained the water begins to rotate also, and lastly, if the glass be suddenly stopped the water will continue to rotate. Suppose further that there was a projection from the side of the glass, pointing towards the centre: when the rotation of the glass commenced, this projection would have to go through the stationary water; there would therefore be an increased pressure of fluid on the side of the projection which was breasting the water and a decreased pressure on the side which was retreating from it; this would be so until the water acquired a rotation as rapid as that of the glass. When the glass was stopped the water would then stream on past the projection and would press on the opposite side to that which had at first suffered the increased pressure; that is to say the side which would have had to breast the stream if the glass had originally been rotated in the opposite direction. If in our minds we replace the glass of water by the horizontal semicircular canal, and the projection by the crista in the ampulla, and if we suppose further that the hair-cells on the crista can appreciate the alterations in the pressure of fluid upon them, we will see, firstly, that they would at once acquaint us of any rotation of the body. Were the body to rotate in the direction of the clock the endolymph would press on one side of the crista; were it to rotate in the reverse direction the endolymph would press on the opposite side; were it to rotate clockwise long enough for the endolymph to acquire the rotation of the body, and then suddenly to stop, the pressure of fluid on the hair-cells of the crista would be similar to that which would be occasioned by the commencement of a rotation against the hands of the clock, and the person would be deceived into thinking

he was rotating in that direction. This then is the explanation of the giddiness which we experience under such circumstances. So far we have considered the horizontal semicircular canals only, but quite similar sensations may be obtained by suitable stimulation of the anterior and posterior canals. These are placed in vertical planes at right angles to one another and are also of course at right angles to the horizontal canal. As any motion in space can be resolved into motions in three planes at right angles, the sensations from the three semicircular canals, when put together in the brain, form an adequate mechanism for the judgment of any motion.

So far we have spoken only of the sense-organs involved in enabling us to co-ordinate our movements. These organs are all united to the central nervous system by nerves. When we trace the vestibular branch of the auditory nerve to the brain we find its course diverges from that of the cochlear branch, or auditory portion proper of the nerve. The vestibular branch, if followed, takes us to that portion of the brain known as the cerebellum, which forms the central organ for the appreciation not only of impulses from the labyrinth, but also for the sensations of which we have spoken from the eyes and from the limbs.

Indeed, mischief in the essential portion of the cerebellum leads to giddiness and inco-ordination of movement as certainly as derangement of the sensations which we have been discussing.

LESSON IX

THE ORGAN OF SIGHT

1. The General Structure of the Eye.—Every sense-organ consists of two parts; the *essential part*, consisting of the structures in which the sensory nerve supplied to the organ terminate, and in which the impulses which pass up that nerve are generated, and the *accessory part*, arranged so as to bring the agent, which affects the organ, to bear upon the essential part. In the case of the eye, the accessory structures are so complicated and their action so striking that they seem, at first sight, to form the greater part of the whole sense-organ. Hence we may, perhaps with advantage, consider the accessory parts first, and then pass on to the essential structures.

The accessory organs, by means of which the physical agent of vision, light, is enabled to act upon the expansion of the optic nerve, comprise three kinds of apparatus: (*a*) a "water camera," the eyeball; (*b*) muscles for moving the eyeball; (*c*) organs for protecting the eyeball, viz. the eyelids, with their lashes, glands, and muscles; the conjunctiva; and the lachrymal gland and its ducts.

The ball, or globe, of the eye is a globular body, moving freely in a chamber, the **orbit**, which is furnished to it by the skull. The optic nerve, the root of which is in

the brain, leaves the skull by a hole at the back of the orbit, and enters the back of the globe of the eye, not in the middle, but on the inner, or nasal, side of the centre. Having pierced the wall of the globe, it spreads out into a very delicate membrane, varying in thickness from $\frac{1}{80}$th of an inch to less than half that amount, which lines the hinder two-thirds of the globe, and is termed the **retina**. This retina is the only organ connected with sensory nervous fibres which can be affected, by any agent, in such a manner as to give rise to the sensation of light.

The **eyeball** is composed, in the first place, of a tough, firm, spheroidal case consisting of fibrous or connective tissue, the greater part of which is white and opaque, and is called the **sclerotic** (Fig. 126, 2). In front, however, this fibrous capsule of the eye, though it does not change its essential character, becomes transparent, and receives the name of the **cornea** (Fig. 126, 1). The front surface of the cornea is covered by an epithelium in which the cells are very similar and similarly arranged to those in the epidermis of the skin. The corneal portion of the case of the eyeball is more convex than the sclerotic portion, so that the whole form of the ball is such as would be produced by cutting off a segment from the front of a spheroid of the diameter of the sclerotic, and replacing this by a segment cut from a smaller, and consequently more convex, spheroid.

The corneo-sclerotic case of the eye is kept in shape by what are termed the *humours*—watery or semi-fluid substances, one of which, the **aqueous humour** (Fig. 126, 7), which is hardly more than water holding a few organic and saline substances in solution, distends the corneal chamber of the eye, while the other, the **vitreous humour** (Fig. 126, 13), which is rather a delicate jelly than a regular fluid, keeps the sclerotic chamber full.

The two humours are separated by the very beautiful, transparent doubly-convex **crystalline lens** (Fig. 126, 12),

denser, and capable of refracting light more strongly than either of the humours. The crystalline lens is composed of fibres having a somewhat complex arrangement,

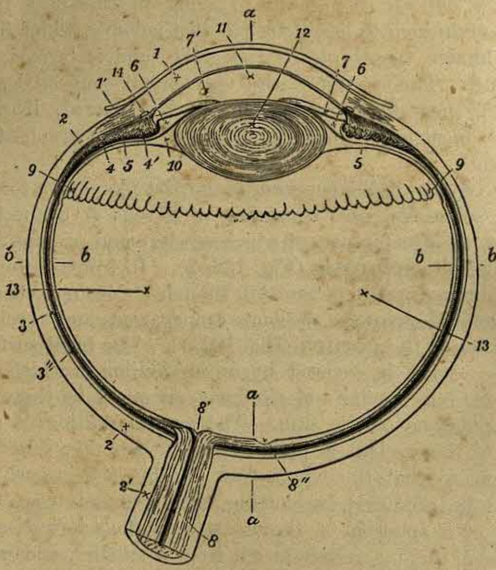


FIG. 126.—HORIZONTAL SECTION OF THE EYEBALL.

1, cornea; 1′, conjunctiva; 2, sclerotic; 2′, sheath of optic nerve; 3, choroid; 3″, rods and cones of the retina; 4, ciliary muscle; 4′, circular portion of ciliary muscle; 5, ciliary process; 6, posterior chamber between 7, the iris and the suspensory ligament; 7′, anterior chamber; 8, artery of retina in the centre of the optic nerve; 8′, centre of blind spot; 8″, macula lutea; 9, ora serrata (this is of course not seen in a section such as this, but is introduced to show its position); 10, space behind the suspensory ligament (canal of Petit); 12, crystalline lens; 13, vitreous humour; 14, marks the position of the ciliary ligament; *a a*, optic axis; *b b*, line of equator of the eyeball.

and is highly elastic. It is more convex behind than in front, and it is kept in place by a delicate, but at the

same time strong membranous frame or **suspensory ligament**, which extends from the edges of the lens to what are termed the **ciliary processes** of the choroid coat (Figs. 126, 5, and 128, *c*). In the ordinary condition of the eye this ligament is kept tense, *i.e.* is stretched pretty tight, and the front part of the lens is consequently flattened.

The **choroid coat** is highly vascular and consists of blood-vessels arranged in a very complex way, bound together with a little connective tissue among which, towards its inner side, are a number of branched connective tissue corpuscles whose cell-substance is loaded with granules of **black pigment** (Fig. 127).

A

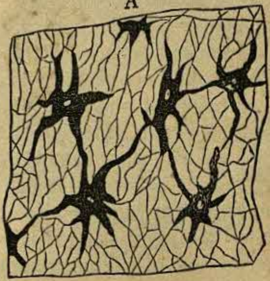


FIG. 127.—PIGMENT CELLS FROM THE CHOROID COAT.

The choroid is in close contact with the sclerotic externally, and internally is in contact with a layer of very peculiar cells, also full of pigment (Fig. 139). But these cells really belong to the retina and will therefore be described later on (p. 424). They are separated from the vitreous humour by the retina only. The choroid lines every part of the sclerotic, except just where the optic nerve enters it at a point below, and to the inner side of the centre of the back of the eye ; but when it reaches

the front part of the sclerotic, its inner surface becomes raised up into a number of longitudinal ridges, with intervening depressions, like the crimped frills of a lady's dress, terminating within and in front by rounded ends, but passing, externally, into the iris. These ridges, which when viewed from behind seem to radiate on all sides from the lens (Figs. 128, *c*, and 126, 5), are the above-mentioned ciliary processes.

The **iris** itself (Figs. 126, 7, and 128, *a*, *b*) is, as has been already said (p. 303), a curtain with a round hole in the middle, the **pupil**, provided with circular and radiating unstriped muscular fibres, and capable of having its central aperture diminished or enlarged by the action of these fibres, the contraction of which, unlike that of other unstriped muscular fibres, is extremely rapid. The edges of the iris are firmly connected with the capsule of the eye, at the junction of the cornea and sclerotic, by the connective tissue which enters into the composition of what used to be called the **ciliary ligament.** The hinder surface of the iris is covered with cells containing a black pigment, similar to that of the choroid coat, and the different colours of eyes depend partly on the varying amount and distribution of pigment in these cells, but chiefly on pigment cells imbedded in and scattered throughout the substance of the iris. Unstriped muscular fibres, having the same attachment in front, spread backwards on to the outer surface of the choroid, constituting the **ciliary muscle** (Fig. 126, 4). If these fibres contract, it is obvious that they will pull the choroid forwards; and as the frame, or suspensory ligament of the lens, is connected with the ciliary processes (which simply form the anterior termination of the choroid), this pulling forward of the choroid brings about a relaxation of the tension of that suspensory ligament, which, as we have just said, is in a resting condition stretched somewhat tight, keeping the front of the lens flattened.

The iris does not hang down perpendicularly into the space between the front face of the crystalline lens and the posterior surface of the cornea, which is filled by the aqueous humour, but applies itself very closely to the anterior face of the lens, so that hardly any interval is left between the two (Figs. 126 and 131).

The retina lines the interior of the eye, being placed between the choroid and vitreous humour, its rods and cones (see pages 415–419) being imbedded in the pigment

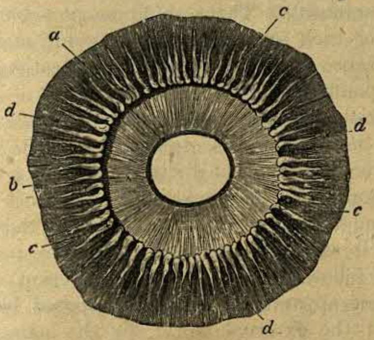


FIG. 128.—VIEW OF FRONT HALF OF THE EYEBALL SEEN FROM BEHIND.

a, circular fibres; *b*, radiating fibres of the iris; *c*, ciliary processes; *d*, choroid. The crystalline lens has been removed.

epithelium lining the former, and its inner limiting membrane touching the latter.

About a third of the distance back from the front of the eye the retina seems to end in a wavy border called the **ora serrata** (Fig. 126, 9), and in reality the nervous elements of the retina do end here, having become considerably reduced before this line is reached. Some of the connective tissue elements however pass on as a delicate kind of membrane at the back of the ciliary processes towards the crystalline lens.

2. The Eye as a Water-Camera.—The impact of the ethereal vibrations upon the sensory expansion, or *essential* part of the visual apparatus alone, is sufficient to give rise to all those *feelings*, which we term sensations of *light* and of *colour*, and further to that feeling of *outness* which accompanies all visual sensation. But, if the retina had a simple transparent covering, the vibrations radiating from any number of distinct luminous points in the external world would affect all parts of it equally, and therefore the feeling aroused would be that of a generally diffused luminosity. There would be no separate feeling of light for each separate radiating point, and hence no correspondence between the visual sensations and the radiating points which aroused them.

It is obvious that, in order to produce this correspondence, or, in other words, to have distinct vision, the essential condition is, that distinct luminous points in the external world shall be represented by distinct feelings of light. And since, in order to produce these distinct feelings, vibrations must fall on separate parts of the retina, it follows that, for the production of distinct vision, some apparatus must be interposed between the retina and the external world, by the action of which distinct luminous points in the latter shall be represented by corresponding points of light on the retina.

In the eye of man and of the higher animals, this *accessory* apparatus of vision is represented by structures which, taken together, act as a biconvex lens, composed of substances which have a much greater refractive power than the air by which the eye is surrounded ; and which throw upon the retina luminous points, which correspond in number, and in position relatively to one another, with those luminous points in the external world from which ethereal vibrations proceed towards the eye. The luminous points thus thrown upon the retina form a picture of the external world—a picture being nothing but lights and shadows, or colours, arranged in such a way as to

correspond with the disposition of the luminous parts of the object represented, and with the qualities of the light which proceeds from them.

That a biconvex lens is competent to produce a picture of the external world on a properly arranged screen, is a fact of which every one can assure himself by simple experiments. An ordinary magnifying glass is a transparent body denser than the air, and convex on both sides. If this **lens** be held at a certain distance from a screen or wall in a dark room, and a lighted candle be placed on the opposite side of it, it will be easy to adjust the distances of candle, lens, and wall, in such a manner that an image of the flame of the candle, upside down, shall be thrown upon the wall.

The spot on which the image is formed is called a **focus**. If the candle be now brought nearer to the lens, the image on the wall will enlarge, and grow blurred and dim, but it may be restored to brightness and definition by moving the lens further from the wall. But if, when the new adjustment has taken place, the candle be moved away from the lens, the image will again become confused, and to restore its clearness, the lens will have to be brought nearer the wall.

Thus a convex lens forms a distinct picture of luminous objects, but only at the focus on the side of the lens opposite to the object; and that focus is nearer when the object is distant, and further off when it is near.

Suppose, however, that, leaving the candle unmoved, a lens with more convex surfaces is substituted for the first, the image will be blurred, and the lens will have to be moved nearer the wall to give it definition. If, on the other hand, a lens with less convex surfaces is substituted for the first, it must be moved further from the wall to attain the same end.

In other words, other things being alike, the more convex the lens the nearer its focus; the less convex, the further off its focus.

If the lens were made of some extensible, elastic substance, like india-rubber, pulling it at the circumference would render it flatter, and thereby lengthen its focus; while, when let go again, it would become more convex, and of shorter focus.

Any material more refractive than the medium in which it is placed, if it have a convex surface, causes the rays of light which pass through the less refractive medium to that surface to converge towards a focus. If a watch-glass be fitted into one side of a box, and the box be then filled with water, a candle may be placed at such a distance outside the watch-glass that an image of its flame shall fall on the opposite wall of the box. If, under these circumstances, a doubly convex lens of glass were introduced into the water in the path of the rays, it would act (though less powerfully than if it were in air) in bringing the rays more quickly to a focus, because glass refracts light more strongly than water does.

A *camera obscura* is a box, into one side of which a lens is fitted, so as to be able to slide backwards and forwards, and thus throw on the screen at the back of the box distinct images of bodies at various distances off. Hence the arrangement just described might be termed a *water camera.*

The eyeball, the most important constituents of which have now been described, is, in principle, a camera of the kind described above—a water camera. That is to say, the sclerotic answers to the box, the cornea to the watch-glass, the aqueous and vitreous humours to the water filling the box, the crystalline to the glass lens, the introduction of which was imagined. The back of the box corresponds with the retina.

But further, in an ordinary camera obscura, it is found desirable to have what is termed a **diaphragm** (that is, an opaque plate with a hole in its centre) in the path of the rays, for the purpose of moderating the light and cutting off the marginal rays which, owing to certain

optical properties of spheroidal surfaces, give rise to defects in the image formed at the focus.

In the eye, the place of this diaphragm is taken by the **iris**, which has the peculiar advantage of being self-regulating: contracting its aperture and admitting less light when the illumination is strong; but dilating its aperture and admitting more light when the light is weak. It thus acts like the various "stops" which a photographer uses according to the varying light.

These changes in the pupil are brought about by the contractions of the circular and radiating muscle-fibres of the iris; contraction of the circular or sphincter fibres makes the pupil smaller or constricts it, contraction of the radiating fibres makes it larger or dilates it. Further conversely relaxation of the circular fibres causes or helps to cause dilation, and relaxation of the radiating fibres causes or helps to cause constriction. Contraction of the circular fibres and so *constriction* of the pupil is brought about by means of fibres of the *oculo-motor* nerve, and contraction of the radiating fibres and so *active dilation* is brought about by means of fibres of the *sympathetic* system and may be induced by stimulation of the sympathetic in the neck.

The constriction of the pupil observed when light falls upon the retina is a reflex action in which the optic nerve provides the path for afferent impulses to a centre in the brain lying beneath the front end of the aqueduct of Sylvius (see Lesson XI), and the third (oculo-motor) cranial nerve (see Lesson XI) provides the path for efferent impulses from the centre to the circular fibres of the iris. The dilation of the pupil when light is withdrawn from the retina is in the main at least due to the cessation of previously acting constrictor impulses.

But the pupil, or aperture of the iris, is either constricted or dilated under many circumstances, other than the mere action of light and darkness on the retina. Thus it is *constricted* when the eye is accommodated for

near objects, during deep sleep, or after the administration of morphia and several other poisons, and in the early stages of the action of alcohol and chloroform. On the other hand the pupil is *dilated* when the eye is accommo dated for distant objects, during violent muscular activity, during dyspnœa, after the administration of atropine and some other poisons, and in the later stages of the action of alcohol and chloroform.

In the case of the action of many poisons the effect produced is due, notably in respect of atropine, to a purely *local action* on the circular (sphincter) fibres of the iris, or on the endings of the nerves in these fibres.

Rays of light passing into the eye undergo a bending or refraction (i) as they enter the eye, at the surface of the cornea, (ii) as they pass through the lens; and as a

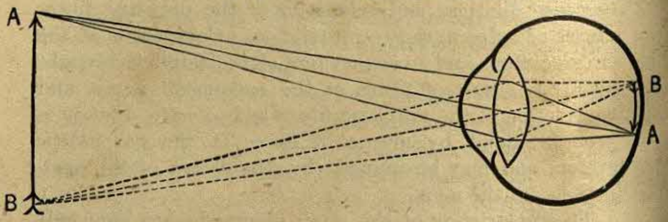


FIG. 129.—THE FORMATION OF AN IMAGE ON THE RETINA.

result of this action of the cornea and lens an image of any object in the external world is formed on the retina.

In the water camera the image brought to a focus on the screen at the back is *inverted*; the image of a tree for instance is seen with the roots upwards and the leaves and branches hanging downwards. The right of the image also corresponds with the left of the object and *vice versâ*. Exactly the same thing takes place in the eye with the image focussed on the retina. It too is inverted. This fact often gives rise to the question, Why then do we see objects in the external world in an erect position and not

also inverted? The answer is simple, and is given in Lesson X.

3. **The Mechanism of Accommodation.**—In the water camera, constructed according to the description given above, there is the defect that no provision exists for adjusting the focus to the varying distances of objects. If the box were so made that its back, on which the image is supposed to be thrown, received distinct images of very distant objects, all near ones would be indistinct. And if, on the other hand, it were fitted to receive the image of near objects, at a given distance, those of either still nearer, or more distant, bodies would be blurred and indistinct. In the ordinary camera this difficulty is overcome by sliding the lenses in and out, a process which is not compatible with the construction of our water camera. But there is clearly one way among many in which this adjustment might be effected—namely, by changing the glass lens; putting in a less convex one when more distant objects had to be pictured, and a more convex one when the images of nearer objects were to be thrown upon the back of the box.

But it would come to the same thing, and be much more convenient, if, without changing the lens, one and the same lens could be made to alter its convexity. This is what actually is done in the adjustment of the eye to distances.

The simplest way of experimenting on the *adjustment* or **accommodation of the eye** is to stick two stout needles upright into a straight piece of wood, not exactly, but nearly in the same straight line, so that, on applying the eye to one end of the piece of wood, one needle (a) shall be seen about six inches off, and the other (b) just on one side of it at twelve inches or more distance.

If the observer look at the needle b, he will find that he sees it very distinctly, and without the least sense of effort; but the image of a is blurred and more or less double. Now let him try to make this blurred image of

the needle *a* distinct. He will find he can do so readily enough, but that the act is accompanied by a sense of effort somewhere in the eye. And in proportion as *a* becomes distinct, *b* will become blurred. Nor will any effort enable him to see *a* and *b* distinctly at the same time.

Multitudes of explanations have been given of this remarkable power of adjustment; but the true solution of the problem has been gained by the accurate determination of the nature of the changes in the eye which

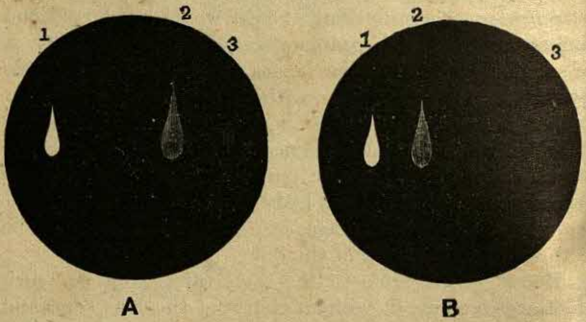


FIG. 130.—DIAGRAM OF THE IMAGES OF A CANDLE-FLAME SEEN BY REFLECTION FROM THE SURFACE OF THE CORNEA AND THE TWO SURFACES OF THE LENS.

A, as seen when the eye is adjusted for a distant object; *B*, as they appear when the eye is fixed on a near object.

accompany the act. When the flame of a taper is held near, and a little on one side of, a person's eye, any one looking into the eye from a proper point of view will see three images of the flame, two upright and one inverted. One upright bright image is reflected from the front of the cornea, which acts as a convex mirror. The second, less bright, proceeds from the front of the crystalline lens, which has the same effect; while the inverted image, which is small and indistinct, proceeds

from the posterior face of the lens, which, being convex backwards, is, of course, concave forwards, and acts as a concave mirror (Fig. 130, *A*).

Suppose the eye to be steadily fixed on a distant object, and then adjusted to a near one in the same line of vision, the position of the eyeball remaining unchanged. Then the upright image reflected from the surface of the cornea, and the inverted image from the back of the lens, will remain unchanged, though it is demonstrable that their size or apparent position must change if either the cornea, or the back of the lens, alter either their form or their

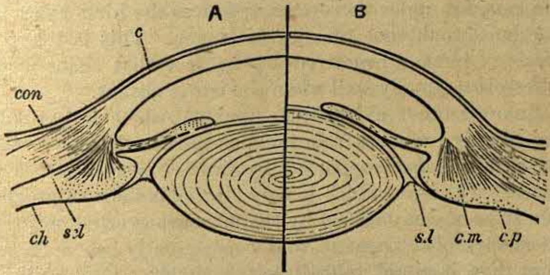


FIG. 131.—THE CHANGES IN THE LENS IN ACCOMMODATION.

A, adjusted for distant; B, for near objects.
c, cornea; *con.* conjunctiva; *scl.* sclerotic; *ch.* choroid; *c.p*, ciliary process; *c.m*, ciliary muscle; *s.l*, suspensory ligament.

position. But the second upright image, that reflected by the front face of the lens, does change both its size and its position; it comes forward and grows smaller (Fig. 130, *B*), proving that the front face of the lens has become more convex. The change of form of the lens is, in fact, that represented in Fig. 131.

For purposes of accurate experiment it is better to employ the images cast by *two* small luminous points placed one above the other. In this case *three pairs* of images are seen by reflection; and it is easier to observe

that the *two* images of the middle pair come nearer together when the eye is accommodated for a near object than it is to observe the slight movement and diminution in size of the *single image* of a candle flame.

These may be regarded as the *facts of adjustment* with which all explanations of that process must accord. They at once exclude the hypothesis (1) that adjustment is the result of the compression of the ball of the eye by its muscles, which would cause a change in the form of the cornea; (2) that adjustment results from a shifting of the lens bodily, for its hinder face does not move; (3) that it results from the pressure of the iris upon the front face of the lens, for under these circumstances the hinder face of the lens would not remain stationary. This last hypothesis is further negatived by the fact that adjustment takes place equally well when the iris is absent.

But one other explanation remains, which is not only exceedingly probable from the anatomical relations of the parts, but is also supported by direct experimental evidence. The lens, which is very elastic, is kept habitually in a state of compression by the pressure exerted on it by its suspensory ligament, and consequently has a flatter form than it would take if left to itself. If the ciliary muscle contracts, it must, as has been seen, relax that ligament, and thereby diminish its pressure upon the lens. The lens, consequently, will become more convex; it will, however, since it is highly elastic, return to its former shape when the ciliary muscle ceases to contract, and allows the choroid to return to its ordinary place.

Hence probably the sense of effort we feel when we adjust for near distances arises from the contraction of the ciliary muscle.

4. The Limits of Accommodation. Use of Spectacles.—Adjustment can take place only within a certain range; this, however, admits of great individual variations.

People possessing ordinary, or as it is called "normal"

sight can adjust their eyes so as to see distinctly objects as near to the eye as five or six inches ; but the image of an object brought nearer than this becomes blurred and indistinct, because the "near limit" of adjustment is then passed. They can also adjust their eyes for objects at a very great distance, the indistinctness of the images of objects very far off being due, not to want of proper focussing, but to the details being lost through the minuteness of the image.

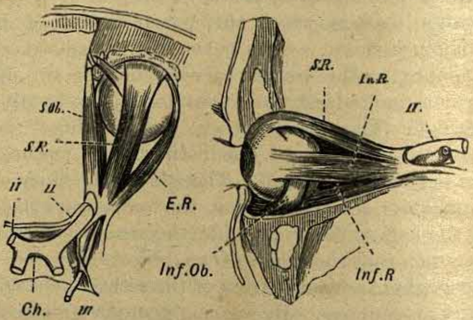
Some people, however, are born with, or at least come to possess, eyes in which the "near limit" of adjustment is much closer. Such persons can see distinctly objects as near to the cornea as even one or two inches ; but they cannot adjust their eyes to objects at any great distance off. Thus many of these "near-sighted" people, as they are called, cannot see distinctly the features of a person only a few feet off. Though their ciliary muscle remains quite relaxed so that the suspensory ligament keeps the lens as flat as possible, the arrangements of the eye are such that the image of an object only a few feet off is brought to a focus in front of the retina, somewhere in the vitreous humour. By wearing **concave** glasses these near-sighted people are able to bring the image of distant objects on to the retina and thus to see them distinctly.

The cause of near-sightedness is not always the same, but in the majority of cases it appears to be due to the bulb of the eye being unusually long from back to front. If, in the water-camera described above, when the lens and object were so adjusted that the image of the object was distinctly focussed on the screen, the box were made longer, so that the screen was moved backwards, the distinctness of the image on it would be lost.

Some people are born really "long-sighted," inasmuch as they can see distinctly only such objects as are quite distant ; and indeed have to contract their ciliary muscles, and so make their lens more convex even to see these. Near objects they cannot see distinctly at all unless they

use **convex** glasses. In such persons the bulb of the eye is generally too short.

A kind of long-sightedness also comes on in old people; but this is different from the above, and is simply due, in the majority of cases at all events, to a loss of power of adjustment. The refractive power of the eye remains the same, but the ciliary muscle fails to work and the lens has become less elastic with years; and hence adjustment for near objects becomes impossible, though distant



A FIG. 132. B

A, the muscles of the right eyeball viewed from above, and B of the left eyeball viewed from the outer side; *S.R*, the superior rectus; *Inf.R*, the inferior rectus; *E.R*, *In.R*, the external rectus; *S.Ob.* the superior oblique; *Inf.Ob.* the inferior oblique; *Ch.* the chiasma of the optic nerves (*II.*); *III*, the third nerve which supplies all the muscles except the superior oblique and the external rectus.

objects are seen as before. For near objects such persons have to use **convex** glasses. They should perhaps be called "old-sighted" rather than "long-sighted."

5. The Muscles of the Eyeball.—The *muscles* which move the eyeball are altogether six in number—four straight muscles, or **recti**, and two oblique muscles, the **obliqui** (Fig. 132). The straight muscles are attached to the back of the bony orbit, round the edges of the hole through which the optic nerve passes, and run straight

forward to their insertions into the sclerotic—one, the **superior rectus**, in the middle line above; one, the **inferior**, opposite it below; and one half-way on each side, the **external** and **internal recti.** The eyeball is completely imbedded in fat behind and laterally; and these muscles turn it as on a cushion; the superior rectus inclining the axis of the eye upwards, the inferior downwards, the external outwards, the internal inwards.

The two oblique muscles, upper and lower, are both attached on the outer side of the ball, and rather behind its centre; and they both pull in a direction from the point of attachment towards the inner side of the orbit—the lower, because it arises here; the upper, because, though it arises along with the *recti* from the back of the orbit, yet, after passing forwards and becoming tendinous at the upper and inner corner of the orbit, it traverses a pulley-like loop of ligament, and then turns downwards and outwards to its insertion. The action of the oblique muscles is somewhat complicated, but their general tendency is to roll the eyeball on its axis, and pull it a little forward and inward.

By means of the contraction of these several muscles the eyeballs may be moved into any desired position and their optic axes (Fig. 126, *a.a.*) directed straight towards any object. This mobility is largely of use in diminishing the necessity for such frequent movements of the whole head as would otherwise be necessary. But the movements are also chiefly of extreme importance as ensuring that any object is seen as *single*, although there is an image of it on the retina of each of the *two eyes*.

6. The Protective Appendages of the Eye.—The **eyelids** are folds of skin containing thin plates of cartilage. They are fringed at the edges with hairs, the **eyelashes**, and contain a series of small glands called **Meibomian glands.** Circularly disposed fibres of striped muscle lie beneath the integuments of the eyelids, and constitute the **orbicularis** muscle which shuts them.

The upper eyelid is raised by a special muscle, the **levator** of the upper lid, which arises at the back of the orbit and runs forwards to end in the lid.

The lower lid has no special depressor.

At the edge of the eyelids the integument becomes continuous with a delicate, vascular and highly nervous mucous membrane, the **conjunctiva**, which lines the interior of the lids and the front of the eyeball, its epithelial layer being even continued over the cornea. The numerous small ducts of a gland which is lodged in the orbit, on the outer side of the ball (Fig. 133, *L.G.*), the **lachrymal gland**, constantly pour its watery secretion into the interspace between the conjunctiva lining the upper eyelid and that covering the ball. On the inner side of the eye is a reddish fold, the **caruncula lachrymalis**, a sort of rudiment of that third eyelid which is to be found in many animals. Above and below, close to the caruncula, the edge of each eyelid presents a minute aperture (the *punctum lachrymale*), the opening of a small canal. The canals from above and below converge and open into the **lachrymal sac**; the upper blind end of a duct (*L.D.*, Fig. 134) which passes down from the orbit to the nose, opening below the inferior turbinal bone (Fig. 69, *h*). It is through this system of canals that the conjunctival mucous membrane is continuous with that of the nose; and it is by them that the secretion of the

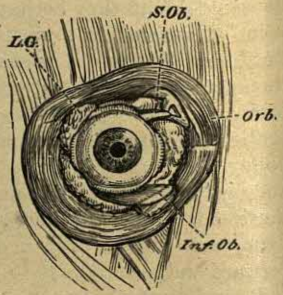


FIG. 133.

The front view of the right eye dissected to show *Orb.* the orbicular muscle of the eyelids; the pulley and insertion of the superior oblique, *S.Ob.*, and the inferior oblique, *Inf.Ob.*; *L.G*, the lachrymal gland.

lachrymal gland is ordinarily carried away as fast as it forms.

But, under certain circumstances, as when the conjunctiva is irritated by pungent vapours, or when painful emotions arise in the mind, the secretion of the lachrymal gland exceeds the drainage power of the lachrymal duct, and the fluid, accumulating between the lids, at length overflows in the form of tears.

7. **The Structure of the Retina.**—If the globe of the eye be cut in two, transversely, so as to divide it into an anterior and a posterior half, the retina will be seen lining the whole of the concave wall of the posterior half as a membrane of great delicacy, and, for the most part, of even texture and smooth surface. But almost exactly opposite the middle of the posterior wall, it presents a slight circular depression of a yellowish hue, the **macula lutea,** or yellow spot (Fig. 135, *m.l.*; Fig. 126, 8″),—not easily seen, however, unless the eye be perfectly fresh,—and, at some distance from this, towards the inner, or nasal, side of the ball, is a radiating appearance, produced by the entrance of the optic nerve and the spreading out of its fibres into the retina.

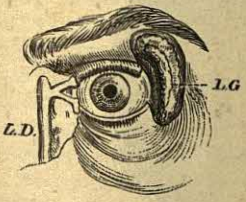


FIG. 134.

A front view of the left eye, with the eyelids partially dissected to show lachrymal gland, *L.G*, and lachrymal duct, *L.D.*

A very thin vertical slice of the retina, in any region except the yellow spot and the entrance of the optic nerve, may be resolved into the structures represented separately in Fig. 136. The one of these (A) occupies the whole thickness of the section, and comprises its essential, or nervous, elements. The outer[1] fourth, or

[1] In the following account of the retina, the parts are described in relation to the eyeball. Thus, that surface of the retina which touches the

rather less, of the thickness of these consists of a vast multitude of minute, either rod-like, or conical bodies, ranged side by side, perpendicularly to the plane of the retina. This is the **layer of rods and cones** (*b c*). From the front ends or bases of the rods and cones very delicate fibres pass, and in each is developed a granule-like or nucleus-like body (*b′ c′*), which forms a

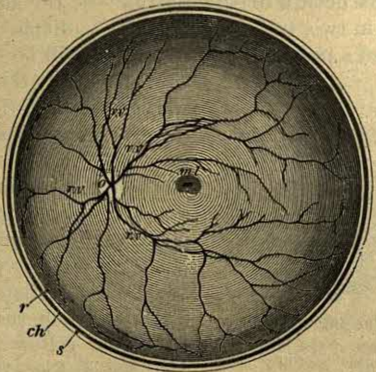


FIG. 135.—THE EYEBALL DIVIDED TRANSVERSELY IN THE MIDDLE LINE AND VIEWED FROM THE FRONT.

s, sclerotic; *ch*, choroid, seen in section only.
r, the cut edges of the retina; *r.v*, vessels of the retina springing from *o*, the optic nerve or blind spot; *m.l*, the yellow spot, the darker spot in its middle being the fovea centralis.

part of what has been termed the **outer nuclear layer.** It is probable that these fibres next pass into and indeed form the close meshwork of very delicate nervous fibres,

vitreous humour, and so is nearer the centre of the eyeball, is called the *inner* surface; and that surface which touches the choroid coat is called the *outer* surface. And so with the structures between these two surfaces; that which is called inner is nearer the vitreous humour, and that which is called outer is nearer the choroid coat. Sometimes *anterior*, or front, is used instead of inner, and *posterior* instead of outer.

the **outer molecular layer**, which is seen at *d d'* (Fig. 136, A). From the inner surface of this meshwork other fibres proceed, containing a second set of granules or nuclei, which forms the **inner nuclear layer** (*f f'*). Inside this layer is a stratum of convoluted fine nervous fibres, the **inner molecular layer** (*g g'*)—and inside this again are numerous **nerve-cells** (*h h'*) constituting the **layer of ganglionic cells**. Processes of these nerve-cells extend, on the one hand, into the layer of convoluted nerve-fibres; and on the other are continuous with the stratum of **fibres of the optic nerve** (*i*).

These delicate nervous structures are supported by a sort of framework of connective tissue of a peculiar kind (B), which extends from an **inner** or **anterior limiting membrane** (*l*), which bounds the retina and is in contact with the vitreous humour, to an **outer** or **posterior limiting membrane** (*a*), which lies at the inner ends, or bases, of the rods and cones near the level of *b' c'* in A. Thus the framework falls short of the nervous substance of the retina, and the rods and cones lie altogether outside of it, wholly unsupported by any connective tissue. They are, however, as we shall see, imbedded in the layer of pigment on which the retina rests (p. 424).

The fibres of the optic nerve spread out between the inner limiting membrane (*l*) and the nerve-cells (*h'*), and the artery which enters along with the optic nerve pierces the centre of the nerve (Fig. 135), and ramifies between the two limiting membranes. Most of the branches run between the inner limiting membrane and the inner nuclear layer (*f f'*). Thus, not only the nervous fibres, but the vessels, are placed altogether in front of the rods and cones.

The structural appearance of the nervous elements of the retina and the seven "layers" into which it may be divided as described above is such as can be made out in any ordinarily stained section. Such a section tells us very little, except in the case of the rods and cones, as to the

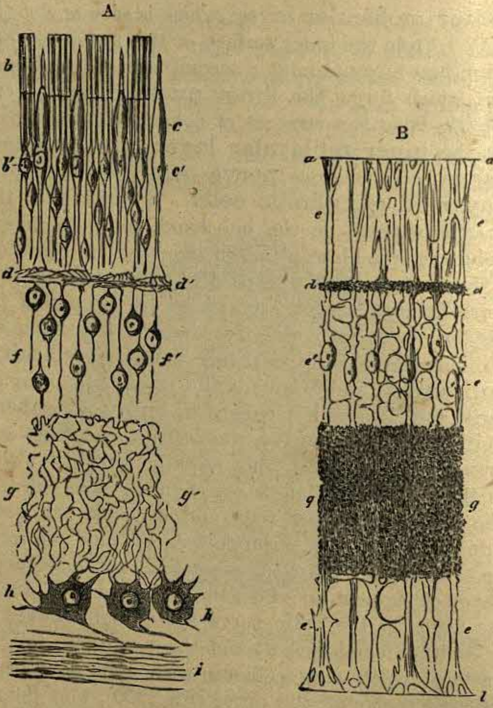


FIG. 136.—DIAGRAMMATIC VIEWS OF THE NERVOUS (A) AND THE CONNECTIVE (B) ELEMENTS OF THE RETINA, SUPPOSED TO BE SEPARATED FROM ONE ANOTHER.

A, the nervous structures—*b*, the rods; *c*, the cones; *b'.c'*, the granules or nuclei of the outer layer, with which these are connected; *d.d'*, interwoven very delicate nervous fibres, from which fine nervous filaments, bearing the inner granules or nuclei, *f.f'*, proceed towards the inner surface; *g.g'*, the continuation of these fine nerves, which become convoluted and interwoven with the processes of the nerve cells *h.h'*; *i.i*, the expansion of the fibres of the optic nerve. B, the connective tissue—*a.a*, external limiting membrane; *e.e*, radial fibres passing to the internal limiting membrane; *e'.e'*, nuclei; *d.d*, the intergranular layer; *g.g*, the molecular layer; *l*, the inner limiting membrane.

(Magnified about 250 diameters.)

real nature of the several structures which give to each layer its characteristic appearance. Still less does it give any clue to the nature of the connections of the successive

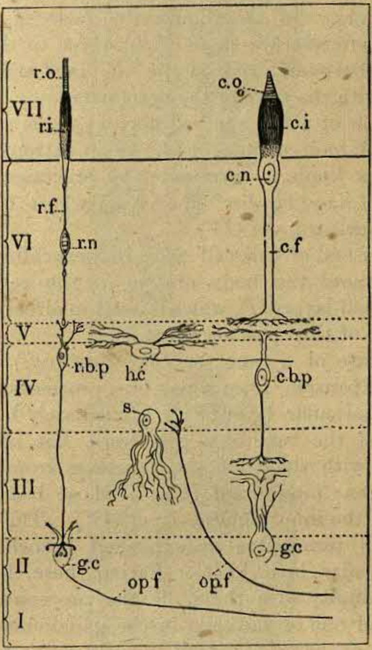


FIG. 137.—DIAGRAM IN ILLUSTRATION OF THE NERVOUS STRUCTURE OF THE RETINA.

I—VII, the several "layers" of the retina.
r.o, *r.i*, outer and inner limbs of a rod; *r.f*, rod fibre; *r.n*, rod nucleus; *r.b.p*, rod bipolar cell; *c.o*, *c.i*, outer and inner limbs of a cone; *c.f*, cone fibre; *c.n*, cone nucleus; *c.b.p*, cone bipolar cell; *g.c*, *g.c*, two cells of the ganglionic cell layer; *op.f*, *op.f*, fibres of optic nerve.

layers with each other by which the *functional continuity* of the rods and cones with the fibres of the optic nerve is brought about. But by the application of very special

methods of staining many details have recently been made out which seem to justify the construction of the following diagrammatic figure (Fig. 137) in illustration of the structure of the retina and of the relationships of its several layers. In this figure the facts of chief and immediate interest are those which refer to the mode of connection between a rod on the one hand and a cone on the other with the fibre of the optic nerve.

In the case of a rod the rod-fibre (*r.f.*) is seen to end in the outer molecular layer (*V*) as an extremely minute knob. This knob is *surrounded by* processes from the outer end of a *rod bipolar cell* (*r.b.p.*) whose body lies in the inner nuclear layer (*IV*).

The inner end of this cell ends in branching processes which *surround* the body of one of the cells in the ganglionic-cell layer (*II*), which is itself in direct continuity with a fibre of the optic nerve (*op.f.*).

In the case of a cone the cone-fibre (*c.f.*) ends as a flattened expansion, from which fine processes extend, in the outer molecular layer (*V*). Immediately below these processes of the base of a cone-fibre, but not actually continuous with them, lie the processes from the outer end of a *cone bipolar cell* (*c.b.p.*) whose body is again situated in the inner nuclear layer (*IV*). The inner end of this cell terminates in expanded branches in the inner molecular layer (*III*). Facing these, but not in actual continuity with them, lie the processes from the outer end of one of the cells in the ganglionic-cell layer (*II*) which, as before, is itself directly connected with a fibre of the optic nerve.

In this way each rod and cone is brought into relationship with a fibre of the optic nerve; but the path of connection in each case shows *two breaks in its structural continuity.* In the case of a rod these breaks lie in the outer molecular layer (*V*) and ganglionic layer (*II*); in the case of a cone they lie in the outer and inner molecular layers respectively (*V* and *III*).

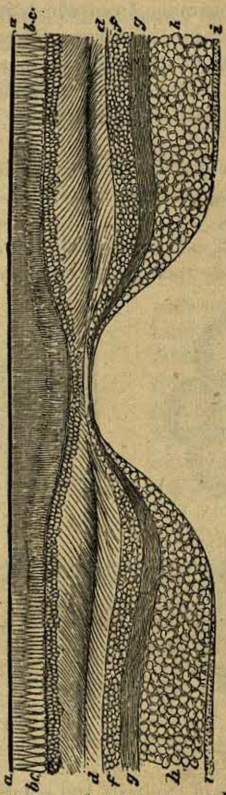


FIG. 138.—A DIAGRAMMATIC SECTION OF THE MACULA LUTEA, OR YELLOW SPOT.

a.a, the pigment of the choroid; *b.c*, rods and cones; *d.d*, outer granular or nuclear layer; *f.f*, inner granular or nuclear layer; *g.g*, molecular layer; *h.h*, layer of nerve cells; *i.i*, fibres of the optic nerve.

(Magnified about 60 diameters.)

In addition to the bipolar cells (*r.b.p.* and *c.b.p.*) which chiefly confer upon the inner nuclear layer (*IV*) the

characteristic appearance from which it derives its name, other cells also occur in this layer. These are shown at *h.c.* and *s.*; but their relationships to the other structural elements of the retina are so uncertain that we must content ourselves with merely drawing attention to their existence.

At the entrance of the optic nerve itself, the nervous fibres predominate, and the rods and cones are absent. In the yellow spot, on the contrary, the cones are abundant and close set, becoming at the same time longer and more slender, while rods are scanty, and are found only

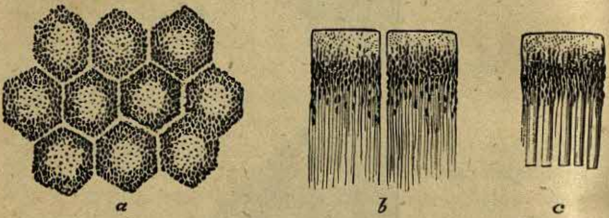


FIG. 139.—PIGMENTED EPITHELIUM OF THE HUMAN RETINA. (MAX SCHULTZE.) Highly magnified.

a, cells seen from the outer (choroidal) surface; *b*, two cells seen sideways, with fine processes on their inner side; *c*, a cell still in connection with the layer of rods of the retina.

towards its margin. In the centre of the *macula lutea* (Fig. 138) the layer of fibres of the optic nerve disappears, and all the other layers, except that of the cones, become extremely thin.

The outer ends of the rods and cones lie buried among certain fine processes of those pigment cells, adjacent to the choroid coat, to whose existence we have previously alluded (pp. 401, 419). When seen from the surface by which they are in contact with the choroid, these cells present the appearance of small black hexagons arranged in a sort of mosaic (Fig. 139, *a*.).

Seen sideways each cell is found to be provided with long, fine, hair-like processes, which stretch in towards the retina and envelop the outer ends of the rods and cones (Fig. 139, *b.c.*).

The rods and cones each consist of two parts, an **outer limb** and an **inner limb**. In the rods the outer limb is quite cylindrical or rod-shaped, and is transversely striated. The inner limb is about as long as the outer, but bulges out slightly in its middle part, so that it forms an elongated cylinder tapering at each end. The outer part of each inner limb is longitudinally striated. The inner end of each inner limb is prolonged into a fine filament, which carries a conspicuous nucleus, often marked transversely, and may be easily traced into the outer molecular layer (Fig. 140, *R.*).

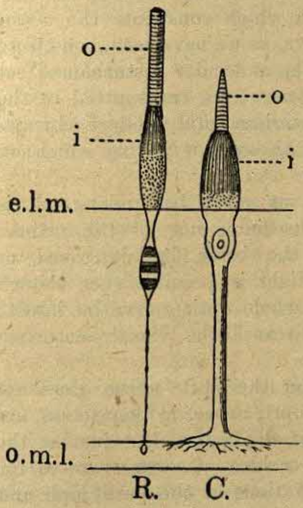


FIG. 140.—DIAGRAM OF A ROD AND OF A CONE.

R, rod; *C*, cone; *o*, outer limb; *i*, inner limb; *e.l.m*, external limiting membrane of retina; *o.m.l*, outer molecular layer of retina.

The outer limb of a cone is much shorter than the outer limb of a rod, and instead of being rod-shaped, is conical and tapering to its outer point; this outer limb is transversely striated. The inner limb of each cone is thicker than the inner limb of a rod, but of the same general shape. It is striated longitudinally in its outer part and carries a large nucleus from which a thick fibre

passes straight into the outer molecular layer of the retina (Fig. 140, *C.*).

8. The Sensation of Light.—The most notable property of the retina is its power of converting the vibrations of ether, which constitute the physical basis of light, into a stimulus to the fibres of the optic nerve. The central ends of these fibres are connected with certain parts of the brain which constitute the *visual sensorium*, just as other parts, as we have seen, constitute the auditory sensorium. The molecular disturbances set up in the fibres of the optic nerve are transmitted to the substance of the visual sensorium, and produce changes in the latter, giving rise to the state of feeling which we call a sensation of light.

The sensation of light, it must be understood, is the work of the visual sensorium, not of the retina; for, if certain parts of the brain be destroyed or affected, no sensation of light is possible even though the retina and indeed the whole optic nerve be intact; blindness is the result, because the visual sensorium cannot work.

Light, falling directly on the optic nerve, does not excite it; the fibres of the optic nerve, in themselves, are as blind as any other part of the body. But just as the peculiar hair-cells of the cochlea, are contrivances for converting the delicate vibrations of the perilymph and endolymph into impulses which can excite the auditory nerves, so the structures in the retina appear to be adapted to convert the infinitely more delicate pulses of the luminiferous ether into stimuli of the fibres of the optic nerve.

9. The "Blind Spot."—The sensibility of the different parts of the retina to light varies very greatly. The point of entrance of the optic nerve is absolutely blind, as may be proved by a very simple experiment. Close the **left** eye, and look steadily with the **right** at the cross on

the page, held at ten or twelve inches distance from the eye.

The black dot will be seen quite plainly, as well as the cross. Now, move the book slowly towards the eye, which must be kept steadily fixed upon the cross; at a certain point the dot will disappear, but, as the book is brought still closer, it will come into view again. It results from optical principles that, in the first position of the book, the image of the dot falls between that of the cross (which throughout lies upon the yellow spot), and the entrance of the optic nerve: while, in the second position, it falls on the point of entrance of the optic nerve itself; and, in the third, it falls on the other side of that point. The three positions of the dot and cross, and of the resulting images of each on the retina, are shown in the accompanying figure, 141.

So long as the image of the spot rests upon the entrance of the optic nerve, it is not perceived, and hence this region of the retina is called the *blind spot*. The experiment proves that the vibrations of the ether are not able to excite the fibres of the optic nerve itself.

10. The Duration of a Luminous Impression.—The impression made by light upon the retina not only remains during the whole period of the direct action of the light, but has a certain duration of its own, however short the time during which the light itself lasts. A flash of lightning is practically instantaneous, but the sensation of light produced by that flash endures for an appreciable period. It is found, in fact, that a luminous impression lasts for about one-eighth of a second; whence it follows,

that if any two luminous impressions are separated by a less interval, they are not distinguished from one another.

For this reason a "Catherine-wheel," or a lighted stick turned round very rapidly by the hand, appears as a circle of fire; and the spokes of a coach wheel at speed are not separately visible, but only appear as a sort of opacity, or film, within the tyre of the wheel.

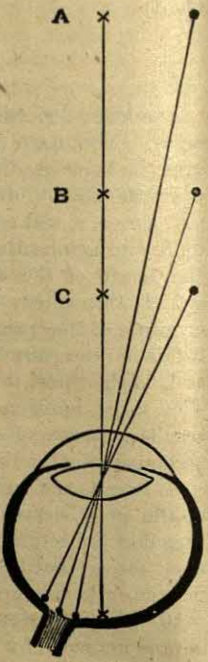


FIG. 141.

The cinematograph is based upon this fact. A series of instantaneous photographs of some object in motion, taken at the rate of many per second, is printed on a long transparent film of celluloid. The film is then passed through a magic-lantern at such a rate that not less than ten of the consecutive photographs are projected on to the screen in each second. At this rate, the impression produced by one photograph has not had time to die out before the next one produces its slightly different later effect. The result is that the consecutive pictures on the screen blend in succession one into the other and so reproduce the appearance of the original moving object.

11. Sensations of Light Produced without the Action of Light.—The sensation of light may be excited by other causes than the impact of the vibrations of the luminiferous ether upon the retina. Thus, an electric

shock sent through the eyeball may give rise to the appearance of a flash of light: and pressure on any part of the retina produces a luminous image, which lasts as long as the pressure, and is called a **phosphene.** If the point of the finger be pressed upon the outer side of the ball of the eye, the eyes being shut, a luminous image—which, in most cases, is dark in the centre, with a bright ring at the circumference (or, as Newton described it, like the "eye" in a peacock's tail-feather)—is seen; and this image lasts as long as the pressure is continued.

The sensation of light is, as already explained, the work of those parts of the brain which, as the visual sensorium, respond to the impulses reaching them through the optic nerve. The retina is the means of supplying the impulses to the sensorium and may be made to do so by light ordinarily, but also by other kinds of stimulation. But the visual sensorium itself may at times be affected by influences other than those which reach it from the retina. In this case also (subjective) luminous sensations of the most vivid and startling kind may be experienced, which give rise to delusive judgments of the most erroneous kind (see p. 442).

12. The Functions of the Rods and Cones.—The last paragraph raises a distinction between the "fibres of the optic nerve" and the "retina" which may not have been anticipated, but which is of much importance.

We have seen that the fibres of the optic nerve ramify in the inner fourth of the thickness of the retina, while the layer of rods and cones forms its outer fourth. The light, therefore, must fall first upon the fibres of the optic nerve, and, only after traversing them, can it reach the rods and cones. Consequently, if the fibrillæ of the optic nerve themselves are capable of being affected by light, the rods and cones can only be some sort of supplementary optical apparatus. But, in fact, it is the rods and cones which are affected by light, while the fibres of the

optic nerve are themselves insensible to it. The evidence on which this statement rests is :—

(i) The blind spot is full of nerve fibres, but has no cones or rods.

(ii) The yellow spot, where the most acute vision is situated, is full of close-set cones, but has no nerve fibres.

(iii) If one goes into a dark room with a single small bright candle, and, looking towards a dark wall, moves the light up and down, close to the outer side of one eye, so as to allow the light to fall very obliquely into the eye, one of what are called **Purkinje's figures** is seen. This is a vision of a series of diverging, branched, dark, sometimes reddish, lines on an illuminated field, and in the interspace of two of these lines is a sort of cup-shaped disc. The branched lines are the images of shadows thrown by the retinal blood-vessels, and the disc is that of the shadow thrown by the edge of the yellow spot. As the candle is moved up and down, the lines shift their position, as shadows do when the light which throws them changes its place.

Now, as the light falls on the inner face of the retina, and the images of the vessels to which it gives rise shift their position as it moves, whatever constitutes the end-organ, through which light stimulates the fibres of the optic nerve, must needs lie on the other, or outer, side of the vessels. But the fibres of the optic nerve lie among the vessels, and the only retinal structures which lie outside them are the nuclear layers and the rods and cones.

(iv) Just as, in the skin, there is a limit of distance within which two points give only one impression, so there is a minimum distance by which two points of light falling on the retina must be separated in order to appear as two. And this distance corresponds pretty well with the diameter of a cone.

The image of the retinal blood-vessels may be also very readily seen by looking at a bright surface, such as the

frosted globe of a burning lamp or a white cloud on a sunny day, through a pinhole in a card. When the card is moved *rapidly from side to side*, but so as to keep the pinhole always within the limits of the *width of the pupil*, the retinal blood vessels are "seen" as a fine branched network of black lines in the bright field of vision.

13. Sensations of Colour and Colour-blindness.—We have spoken of the eye so far simply as the instrument by which luminous sensations arise when the retina is stimulated; as an instrument which enables us to appreciate the position of a source of light, and differences in the intensity of the light which it emits or reflects, and hence to perceive objects in the world around us as regards their position, shape and size. But the objects we see are characterised by something more than mere shape and size; they differ also in respect of what we call their colour.

When we look at a rainbow we are conscious of seven broadly distinct kinds of colour-sensations; these are red, orange, yellow, green, blue, indigo-blue and violet, and when ordinary white light is passed through a prism and then allowed to fall into the eye we experience the same seven coloured sensations. The prism has, in fact, resolved the light into its several coloured constituents, and these are known as the "colours of the spectrum." Each colour which we recognise as such is characterised, just as in the case of sounds, by certain qualities; these are (i) **Hue**, or colour as we ordinarily use the word to denote what we call reds, greens, blues and so on. This quality is dependent on the wave-length of the ethereal vibrations which are giving rise to the sensation, and hence corresponds to the "pitch" of a sound. (ii) **Intensity** or **brightness**. This depends on the amount of light which falls on the retina in a given time and corresponds to the loudness of a sound. (iii) **Saturation**, or the amount of admixture with white light. Thus we speak of a colour as being "pale" if mixed with much

white and as being "deep," "rich," or "full" if highly saturated, *i.e.* unmixed with white.

The colours of objects depend on the power they possess of absorbing some of the constituents of ordinary white light and allowing others to pass or to be reflected. Thus a piece of glass is red if it allows the red rays to pass to the eye and stops the others. Similarly the colour of an *opaque* red object is due to an absorption of the spectral colours other than red by the superficial layer of the object and the reflection of the unabsorbed red rays from its internal parts.

When white light has been split up into its coloured constituents by means of a prism, these may be gathered up again by a second prism, suitably placed, and recombined to make white light. In this experiment the several colours of the spectrum are *mixed* once more after having been sorted out or separated, and the mixing is a *physical* process. But colours may also be mixed *physiologically* by taking advantage of that persistence of luminous impressions to which we have already drawn attention (p. 423). Thus if the several colours of the spectrum are painted in sectors on a circular disc and the disc is made to spin rapidly round its centre, the sensations due to each colour are blended together and the disc appears white. The instrument used in this mode of mixing colours is called a "*colour top*" and the principle it embodies will be not unfamiliar to most people in the form of a common toy.

By the use of a colour top it is at once possible to mix not merely all the spectral colours but any two or three of them. Experimenting in this way with pairs of colours we find that there are several pairs which when mixed, in the right proportions, give rise to the sensation of white: thus red and green, orange and blue, yellow and indigo-blue, greenish-yellow and violet. Colours which when mixed in this way in pairs give white are known as **complementary colours,** and

every colour has some other colour which is complementary to it. If instead of mixing the colours in pairs we mix them in threes, then it becomes still more easy to produce a resultant white. Thus by mixing red, green and blue, with due regard to the relative amount and intensity of each, an excellent white is readily obtained. But these three colours enable us to do more than merely produce white. By properly adjusting the proportions of each on the disc of the colour-top we can easily produce an orange and a yellow, as also a violet. In other words these three colours and their mixtures give rise to all the several kinds of colour-sensation which we derive from a spectrum. Further, by suitable mixture of these colours, together with white or black, we can produce the other colours which we see in natural objects around us but which are wanting in the spectrum. Thus purple is extremely common in the world and can be made at once by mixing red and blue. Hence these three colours have come to be regarded as **primary colours**, and we may speak of the sensations to which they give rise as primary sensations.

The foregoing considerations lead at once to the view that all our sensations of colour may be regarded as the outcome of a very limited number (three) of simple or **primary sensations** corresponding to **red, green** and **blue.** In accordance with this fact a theory has been put forward [1] that there are in the visual apparatus three kinds of nervous structure of which each corresponds to one of the primary colours and is most easily set in action by one of these colours. Thus the stimulation of one of them gives rise to one of the primary sensations, the *simultaneous* stimulation of all three to the same extent gives rise to the sensation of white and their simultaneous stimulation to varying degrees gives rise to all the other

[1] This theory was first propounded by an Englishman, Dr. Thomas Young, the originator of the undulatory theory of light. In later times it was adopted and amplified by Helmholtz, and is therefore known as the Young-Helmholtz theory.

sensations of colour of which we are at any time conscious.

Another theory has been started in whose support very much may be said.[1] It resembles the previous one inasmuch as it also assumes that all our sensations of colour result from a limited number of primary sensations. But it differs in the number and selection of the primary colours. Thus according to this theory there are **three pairs** of primary sensations arising from three pairs of primary colours : these are **red-green, yellow-blue, white-black.** Further, this theory assumes the existence in the visual apparatus of three kinds of **visual substance** of which each corresponds to one of the above pairs of colours, and it assumes that these substances may be made, somewhat in the same way as the sensitive salts on a photographic plate, to undergo a *destructive* change by the action of light in such a way as to give rise to the sensations of red, yellow and white. Finally it supposes that the other three antagonistic sensations arise from the subsequent *constructive* building up again of their visual substances which must take place as soon as the luminous cause of their destructive change has been removed. Thus the breaking down of the red-green visual substance gives rise to the sensation of red, and its building up again to the sensation of green, and similarly for the other two pairs.

Both these theories attempt to account for observed facts, and each goes a long way in doing so ; but neither of them accounts completely for all the facts of colour vision. Neither may we enter into any discussion of their respective merits, for such discussion would be useless if it were not lengthy and detailed, and its intricacy would be still further out of place in an elementary work which excludes as far as possible all debatable matter.

The excitability of the retina is readily exhausted.

[1] This is the theory of Hering.

Thus, looking at a bright light rapidly renders the part of the retina on which the light falls, insensible; and on looking from the bright light towards a moderately-lighted surface, a dark spot, arising from a temporary blindness of the retina in this part, appears in the field of view. If the bright light be of one colour, the part of the retina on which it falls becomes insensible to the rays of that colour, but not to the other rays of the spectrum. This is the explanation of the appearance of what are called **after-images**. For example, if, as in the form in which the experiment is most commonly made, a bright *red* wafer be stuck upon a sheet of white paper, and steadily looked at for some time with one eye, when the eye is turned aside to the white paper a *greenish* spot will appear, of about the size and shape of the wafer. The red image has, in fact, fatigued the part of the retina on which it fell for red light, but has left it sensitive to the remaining coloured rays of which white light is composed. But we know that if from the variously coloured rays which make up the spectrum of white light we take away all the red rays, the remaining rays together make up a sort of green. So that, when white light falls upon this part, the red rays in the white light having no effect, the result of the operation of the others is a greenish hue. The colour of the after-image is thus of necessity *complementary* to that of the object looked at. If the wafer be *green*, the after-image is of course *red*.

Colour-blindness.—Most people agree very closely as to differences between different colours and different parts of the spectrum. But there are exceptions. Thus a certain number of persons see very little difference between the colour which most people call red, and that which most people call green. Such *colour-blind* persons are unable to distinguish between the leaves of a cherry-tree and its fruit by the colour of the two; they are only aware of a difference of shape between the two. Cases of this "red-blindness" or "red-

green" blindness are not uncommon; but another form of colour-blindness in which blue and yellow cannot be distinguished from each other is much more rare; and still rarer, though of undoubted occurrence, are the cases of those who are *wholly* colour-blind, *i.e.* to whom all colours are mere shades of one tint.

This peculiarity of colour-blindness is simply unfortunate for most people, but it may be dangerous if unknowingly possessed by engine-drivers or sailors, particularly since red-green colour-blindness is most common and red and green are exactly the two colours ordinarily used for signals. It probably arises either from a defect in the retina, which renders that organ unable to respond to different kinds of luminous vibrations, and consequently insensible to red, yellow, or other rays, as the case may be; or the fault may lie in the visual sensorium itself.

For ordinary purposes colour perception may be most easily and successfully tested by asking the person under examination to make matches between skeins of coloured wool. In this way it is found that a red-green colour-blind person matches a red with a green skein. A more satisfactory test than the matching of wools is furnished by the use of coloured lights, and for a detailed investigation of the sensations of the colour-blind more exact observations by help of the spectrum are necessary.

The phenomena of colour-blindness can, to a certain extent at least, be explained according to either of the theories of colour-vision which have been given above. Thus by the Young-Helmholtz theory a red-green colour-blind person lacks either the red-perceiving or the green-perceiving structures normally present either in the retina or the visual sensorium. According to the theory of Hering they lack the red-green visual substance.

LESSON X

THE COALESCENCE OF SENSATIONS WITH ONE ANOTHER AND WITH OTHER STATES OF CONSCIOUSNESS

1. **Sensations may be Simple or Composite.**—In explaining the functions of the sensory organs, we have hitherto confined ourselves to describing the means by which the physical agent of a sensation is enabled to irritate a given sensory nerve; and to giving some account of the simple sensations which are thus evolved.

Simple sensations of this kind are such as might be produced by the irritation of a single nerve-fibre, or of several nerve-fibres by the same agent. Such are the sensations of contact, of warmth, of sweetness, of an odour, of a musical note, of whiteness, or redness.

But very few of our sensations are thus simple. Most of even those which we are in the habit of regarding as simple, are really compounds of different simultaneous sensations, or of present sensations with past sensations, or with those feelings of relation which form the basis of judgments. For example, in the preceding cases it is very difficult to separate the sensation of contact from the judgment that something is touching us; of sweetness, from the idea of something in the mouth; of sound or light, from the judgment that something outside us is shining or sounding.

The sensations of smell are those which are least complicated by accessories of this sort. Thus, particles

of musk diffuse themselves with great rapidity through the nasal passages and give rise to the sensation of a powerful odour. But beyond a broad notion that the odour is in the nose, this sensation is unaccompanied by any ideas of locality and direction. Still less does it give rise to any conception of form, or size, or force, or of succession, or contemporaneity. If a man had no other sense than that of smell, and musk were the only odorous body, he could have no sense of *outness*—no power of distinguishing between the external world and himself.

Contrast this with what may seem to be the equally simple sensation obtained by drawing the finger along the table, the eyes being shut. This act gives one the sensation of a flat, hard surface outside one's self, which sensation appears to be just as simple as the odour of musk, but is really a complex state of feeling compounded of—

(*a*) Pure sensations of contact.

(*b*) Pure muscular sensations of two kinds,—the one arising from the resistance of the table, the other from the actions of those muscles which draw the finger along.

(*c*) Ideas of the order in which these pure sensations succeed one another.

(*d*) Comparisons of these sensations and their order, with the recollection of like sensations similarly arranged, which have been obtained on previous occasions.

(*e*) Recollections of the impressions of extension, flatness, &c., made on the organ of vision when these previous tactile and muscular sensations were obtained.

Thus, in this case, the only pure sensations are those of contact and muscular action. The greater part of what we call the sensation is a complex mass of present and recollected sensations and judgments.

Should any doubt remain that we do thus mix up our sensations with our judgments into one indistinguishable whole, shut the eyes as before, and, instead of touching

the table with the finger, take a round lead pencil between the fingers, and draw that along the table. The "sensation" of a flat hard surface will be just as clear as before; and yet all that we touch is the round surface of the pencil, and the only pure sensations we owe to the table are those afforded by the muscular sense. In fact, in this case, our "sensation" of a flat hard surface is entirely a judgment based upon what the muscular sense tells us is going on in certain muscles.

A still more striking case of the tenacity with which we adhere to complex judgments, which we conceive to be pure sensations, and are unable to analyse otherwise than by a process of abstract reasoning, is afforded by our sense of roundness.

Any one taking a marble between two fingers will say that he feels it to be a single round body; and he will probably be as much at a loss to answer the question how he knows that it is round, as he would be if he were asked how he knows that a scent is a scent.

Nevertheless, this notion of the roundness of the marble is really a very complex judgment, and that it is so may be shown by a simple experiment. If the index and middle fingers be crossed, and the marble placed between them, so as to be in contact with both, it is utterly impossible to avoid the belief that there are two marbles instead of one. Even looking at the marble, and seeing that there is only one, does not weaken the apparent proof derived from touch that there are two.[1]

The fact is, that our notions of singleness and roundness are, really, highly complex judgments based upon a few simple sensations; and when the ordinary conditions of those judgments are reversed, the judgment is also reversed.

1 A ludicrous form of this experiment is to apply the crossed fingers to the end of the nose, when it at once appears double; and in spite of the absurdity of the conviction the mind cannot expel it so long as the sensations last.

With the index and the middle fingers in their ordinary position, it is of course impossible that the outer sides of each should touch opposite surfaces of one spheroidal body. If, in the natural and usual position of the fingers, their outer surfaces simultaneously give us the impression of a spheroid (which itself is a complex judgment), it is in the nature of things that there must be two spheroids. But, when the fingers are crossed over the marble, the outer side of each finger is really in contact with a spheroid; and the mind, taking no cognizance of the crossing, judges in accordance with its universal experience, that two spheroids, and not one give rise to the sensations which are perceived.

2. **Judgments are Delusive, not Sensations.**—Phenomena of the kind described in the preceding section are not uncommonly called *delusions of the senses;* but there is no such thing as a fictitious, or delusive, sensation. A sensation must exist to be a sensation, and if it exists, it is real and not delusive. But the judgments we form respecting the causes and conditions of the sensations of which we are aware, are very often erroneous and delusive enough; and such judgments may be brought about in the domain of every sense, either by artificial combinations of sensations, or by the influence of unusual conditions of the body itself. The latter give rise to what are called *subjective sensations.*

Mankind would be subject to fewer delusions than they are, if they constantly bore in mind their liability to false judgments due to unusual combinations, either artificial or natural, of true sensations. Men say, "I felt," "I heard," "I saw" such and such a thing, when, in ninety-nine cases out of a hundred, what they really mean is, that they judge that certain sensations of touch, hearing, or sight, of which they were conscious, were caused by such and such things.

3. **Subjective Sensations.**—Among *subjective sensations* within the domain of touch, are the feelings of creeping

and the prickling of the skin, which may sometimes be due to certain states of the circulation, but probably more frequently to processes going on in the central nervous system. The subjective evil smells and bad tastes which accompany some diseases are, in a similar way, very probably due to disturbances in the brain in the central end-organs of the nerves of smell and taste.

Many persons are liable to what may be called *auditory spectra*—music of various degrees of complexity sounding in their ears, without any external cause, while they are wide awake. I know not if other persons are similarly troubled, but in reading books written by persons with whom I am acquainted, I am sometimes tormented by hearing the words pronounced in the exact way in which these persons would utter them, any trick or peculiarity of voice, or gesture, being, also, very accurately reproduced. And I suppose that everyone must have been startled, at times, by the extreme distinctness with which his thoughts have embodied themselves in apparent voices.

The most wonderful exemplifications of subjective sensation, however, are afforded by the organ of sight.

Any one who has witnessed the sufferings of a man labouring under *delirium tremens* (a disease produced by excessive drinking), from the marvellous distinctness of his visions, which sometimes take the forms of devils, sometimes of creeping animals, but almost always of something fearful or loathsome, will not doubt the intensity of subjective sensations in the domain of vision.

But in order that illusive visions of great distinctness should appear, it is not necessary for the nervous system to be thus obviously deranged. People in the full possession of their faculties, and of high intelligence, may be subject to such appearances, for which no distinct cause can be assigned. An excellent illustration of this is the famous case of Mrs. A. given by Sir David Brewster, in his *Natural Magic*. This lady was subject to un-

usually vivid auditory and ocular spectra. Thus on one occasion she saw her husband standing before her and looking fixedly at her with a serious expression, though at the time he was at another place. On another occasion she heard him repeatedly call her, though at the time he was not anywhere near. On another occasion she saw a cat in the room lying on the rug ; and so vivid was the illusion that she had great difficulty in satisfying herself that really there was no cat there. The whole account is well worthy of perusal.

It is obvious that nothing but the singular courage and clear intellect of Mrs. A. prevented her from becoming a mine of ghost stories of the most excellently authenticated kind. And the particular value of her history lies in its showing, that the clearest testimony of the most unimpeachable witness may be quite inconclusive as to the objective reality of something which the witness has seen.

Mrs. A. undoubtedly saw what she said she saw. The evidence of her eyes as to the existence of the apparitions, and of her ears to those of the voices, was, in itself, as perfectly trustworthy as their evidence would have been had the objects really existed. For there can be no doubt that exactly those parts of her retina which would have been affected by the image of a cat, and those parts of her auditory organ which would have been set vibrating by her husband's voice, or rather the portions of the sensorium with which those organs of sense are connected, were thrown into a corresponding state of activity by some internal cause.

What the senses testify is neither more nor less than the fact of their own affection. As to the cause of that affection they really say nothing, but leave the mind to form its own judgment on the matter. A hasty or superstitious person in Mrs. A.'s place would have formed a wrong judgment, and would have stood by it on the plea that "she must believe her senses."

4. Delusions of Judgment.—The delusions of the judgment, produced not by abnormal conditions of the body, but by unusual or artificial combinations of sensations, or by suggestions of ideas, are exceedingly numerous, and, occasionally, are not a little remarkable.

Some of those which arise out of the sensation of touch have already been noted. We do not know of any produced through smell or taste, but hearing is a fertile source of such errors.

What is called **ventriloquism** (speaking from the belly), and is not uncommonly ascribed to a mysterious power of producing voice somewhere else than in the larynx, depends entirely upon the accuracy with which the performer can simulate sounds of a particular character, and upon the skill with which he can suggest a belief in the existence of the causes of these sounds. Thus, if the ventriloquist desire to create the belief that a voice issues from the bowels of the earth, he imitates with great accuracy the tones of such a half-stifled voice, and suggests the existence of some one uttering it by directing his answers and gestures towards the ground. These gestures and tones are such as would be produced by a given cause; and no other cause being apparent, the mind of the bystander insensibly judges the suggested cause to exist.

The delusions of the judgment through the sense of sight—*optical delusions*, as they are called—are more numerous than any others, because such a great number of what we think to be simple visual sensations are really very complex aggregates of visual sensations, tactile sensations, judgments, and recollections of former sensations and judgments.

It will be instructive to analyse some of these judgments into their principles, and to explain the delusions by the application of these principles.

5. The Inversion of the Visual Image.—*When we look at an external object, the image of the object falls on*

the retina at the end of the visual axis, i.e. *a line joining the object and the retina and traversing a particular region of the centre of the eye. Conversely, when a part of the retina is excited, by whatever means, the sensation is referred by the mind to some cause outside the body in the direction of the visual axis.*

When we look at an external object which is felt by the touch to be in a given place, the image of the object falls upon a certain part of the retina. Conversely, when a part of the retina is excited, by whatever means, the sensation is referred by the mind to some cause outside the body occupying such a position that its image would fall on that part.

It is for this reason that when a phosphene is created by pressure, say on the outer and lower side of the eyeball, the luminous image appears to lie above, and to the inner side of, the eye. Any external object which could produce the sense of light in the part of the retina pressed upon must, owing to the inversion of the retinal images (see p. 408), in fact occupy this position; and hence the mind refers the light seen to an object in that position.

The same kind of explanation is applicable to the apparent paradox that, while all the pictures of external objects are certainly inverted on the retina by the refracting media of the eye, we nevertheless see them upright. It is difficult to understand this, until one reflects that the retina has, in itself, no means of indicating to the mind which of its parts lies at the top, and which at the bottom; and that the mind learns to call an impression on the retina high or low, right or left, simply on account of the association of such an impression with certain coincident tactile impressions. In other words, when one part of the retina is affected, the object causing the affection is found to be near the right hand; when another, the left; when another, the hand has to be raised to reach the object; when yet another, it has to be depressed to reach it. And thus the several impressions on the

retina are called right, left, upper, lower, quite irrespectively of their real positions, of which the mind has, and can have, no cognizance.

6. **Single Objects give rise to Single Images.**—*When an external body is ascertained by touch to be simple, it forms but one image on the retina of a single eye; and when two or more images fall on the retina of a single eye, they ordinarily proceed from a corresponding number of bodies which are distinct to the touch.*

Conversely, the sensation of two or more images is judged by the mind to proceed from two or more objects.

If two pin-holes be made in a piece of cardboard at a distance less than the diameter of the pupil, and a small object like the head of a pin be held pretty close to the eye, and viewed through these holes, two images of the head of the pin will be seen. The reason of this is, that the rays of light from the head of the pin are split by the card into two minute pencils, which pass into the eye on either side of its centre, and, on account of the nearness of the pin to the eye, meet the retina before they can be united again and brought to one focus. Hence they fall on different parts of the retina, and each pencil of rays being very small, makes a tolerably distinct image of its own of the pin's head on the retina. Each of these images is now referred outward (p. 444) and two pins are apparently seen instead of one. A like explanation applies to *multiplying glasses* and *doubly refracting* crystals, both of which, in their own ways, split the pencils of light proceeding from a single object into two or more separate bundles. These give rise to as many images, each of which is referred by the mind to a distinct external object.

7. **The Judgment of Distance and Size by the Brightness and Size of Visual Images.**—*Certain visual phenomena ordinarily accompany those products of tactile sensation to which we give the name of size, distance, and form. Thus, other things being alike, the space of the retina*

covered by the image of a large object is larger than that covered by a small object; while that covered by an object when near is larger than that covered by the same object when distant; and, other conditions being alike, a near object is more brilliant than a distant one. Furthermore, the shadows of objects differ according to the forms of their surfaces, as determined by touch.

Conversely, if these visual sensations can be produced, they inevitably suggest a belief in the existence of objects competent to produce the corresponding tactile sensations.

What is called *perspective*, whether *solid* or *aërial* in drawing, or painting, depends on the application of these principles. It is a kind of visual ventriloquism—the painter putting upon his canvas all the conditions requisite for the production of images on the retina, having the size, relative form, and intensity of colour of those which would actually be produced by the objects themselves in nature. And the success of his picture, as an imitation, depends upon the closeness of the resemblance between the images it produces on the retina, and those which would be produced by the objects represented.

To most persons the image of a pin, at three or four inches from the eye, appears blurred and indistinct—the eye not being capable of adjustment to so short a focus. If a small hole be made in a piece of card, the circumferential rays which cause the blur are cut off, and the image becomes distinct. But at the same time it is magnified, or looks bigger, because the image of the pin, in spite of the loss of the circumferential rays, occupies a much larger extent of the retina when close than when distant. All convex glasses produce the same effect—while concave lenses diminish the apparent size of an object, because they diminish the size of its image on the retina.

Objects, as is well known, appear larger when seen in a fog. In this case the actual size of the image on the retina is the same as if there were no fog. But the indis-

tinctness with which the object is seen leads to the wrong conclusion that it is situated at some considerable distance from the observer. Hence the judgment is formed that the object is large, because if it were not large it could not, *at the apparently greater distance*, produce an image on the retina of the size it does.

The moon, or the sun, when near the horizon appears very much larger than when it is high in the sky. This is usually said to be due to the fact that when in the latter position we have nothing to compare it with, and the small extent of the retina which its image occupies suggests small absolute size. But as it sets, we see it passing behind great trees and buildings which we know to be very large and very distant, and yet it occupies a larger space on the retina than they do. Hence the vague suggestion of its larger size. But this has really very little to do with the delusion, for the appearance is the same if the sun or moon is seen near the horizon over the open sea, where no comparison with other objects is possible. Probably one cause of the delusion is that when low down the sun or moon is seen less distinctly, on account of mist and vapour, and thus "looks" large for the same reason that a man seen in a fog appears unduly big, or the delusion may be due to the fact that to most people the distance from them to the horizon appears greater than the distance straight above them to the summit of the vault of the heavens (or the zenith). Hence though the actual size of the image of the sun or moon on the retina is the same whether they be low down or high up, the idea that they are further off when low down suggests that they are of greater size.

8. Judgment of Form by Shadows.—If a convex surface be lighted from one side, the side towards the light is bright—that turned from the light, dark, or in shadow; while a concavity is shaded on the side towards the light, bright on the opposite side.

If a new half-crown, or a medal with a well-raised head

upon its face, be lighted sideways by a candle, we at once know the head to be raised (or a *cameo*) by the disposition of the light and shade; and if an *intaglio*, or medal on which the head is hollowed out, be lighted in the same way, its nature is as readily judged by the eye.

But now, if either of the objects thus lighted be viewed with a convex lens, which inverts its position, the light and dark sides will be reversed. With the reversal the judgment of the mind will change, so that the cameo will be regarded as an intaglio, and the intaglio as a cameo; for the light still comes from where it did, but the cameo appears to have the shadows of an intaglio, and *vice versâ*. So completely, however, is this interpretation of the facts a matter of judgment, that if a pin be stuck beside the medal so as to throw a shadow, the pin and its shadow, being reversed by the lens, will suggest that the direction of the light is also reversed, and the medals will seem to be what they really are.

9. The Judgment of Changes of Form.—*Whenever an external object is watched rapidly changing its form, a continuous series of different pictures of the object is impressed upon the same spot of the retina.*

Conversely, if a continuous series of different pictures of one object is impressed upon one part of the retina, the mind judges that they are due to a single external object, undergoing changes of form.

This is the principle of the curious toy called the *thaumatrope*, or "zootrope," or "wheel of life," by the help of which, on looking through a hole, one sees images of jugglers throwing up and catching balls, or boys playing at leapfrog over one another's backs. This is managed by painting at intervals, on a disc of card, figures and jugglers in the attitudes of throwing, waiting to catch, and catching; or boys "giving a back," leaping, and coming into position after leaping. The disc is then made to rotate before an opening, so that each image shall be presented for an instant, and follow its predecessor before

the impression of the latter has died away. The result is that the succession of different pictures irresistibly suggests one or more objects undergoing successive changes—the juggler seems to throw the balls, and the boys appear to jump over one another's backs. The same explanation holds good for the cinematograph. (See p. 428).

10. Single Vision with Two Eyes. Corresponding Points.—*When an external object is ascertained by touch to be single, the centres of its retinal images in the two eyes fall upon the centres of the yellow spots of the two eyes, when both eyes are directed towards it; but if there be two external objects, the centres of both their images cannot fall, at the same time, upon the centres of the yellow spots.*

Conversely, when the centres of two images, formed simultaneously in the two eyes, fall upon the centres of the yellow spots, the mind judges the images to be caused by a single external object; but if not, by two.

This seems to be the only admissible explanation of the facts, that an object which appears single to the touch and when viewed with one eye, also appears single when it is viewed with both eyes, though two images of it are necessarily formed; and on the other hand, that when the centres of the two images of one object do not fall on the centres of the yellow spots, both images are seen separately, and we have double vision. In squinting, the axes of the two eyes do not converge equally towards the object viewed. In consequence of this, when the centre of the image formed by one eye falls on the centre of the yellow spot, the corresponding part of that formed by the other eye does not, and double vision is the result.

For simplicity's sake we have supposed the images to fall on the centre of the yellow spot. But though vision is distinct only in the yellow spot, it is not absolutely limited to it; and it is quite possible for an object to be seen as a single object with two eyes, though its images fall on the two retinas outside the yellow spots. All that

is necessary is that the two spots of the retinas on which the images fall should be similarly disposed towards the centres of their respective yellow spots. Any two points of the two retinas thus similarly disposed towards their respective yellow spots (or more exactly to the points in which the visual axes end), are spoken of as **corresponding points**; and any two images covering two corresponding areas are conceived of as coming from a single object. It is obvious that the inner (or nasal) side of one retina *corresponds* to the outer (or cheek) side of the other.

11. The Judgment of Solidity.—*When a body of moderate size, ascertained by touch to be solid, is viewed with both eyes, the images of it, formed by the two eyes, are necessarily different (one showing more of its right side, the other of its left side). Nevertheless, they coalesce into a common image, which gives the impression of solidity.*

Conversely, if the two images of the right and left aspects of a solid body be made to fall upon the retinas of the two eyes in such a way as to coalesce into a common image, they are judged by the mind to proceed from the single solid body which alone, under ordinary circumstances, is competent to produce them.

The *stereoscope* is constructed upon this principle. Whatever its form, it is so contrived as to throw the images of two pictures of a solid body, such as would be obtained by the right and left eye of a spectator, on to such parts of the retinas of the person who uses the stereoscope as would receive these images, if they really proceeded from one solid body. The mind immediately judges them to arise from a single external solid body, and sees such a solid body in place of the two pictures.

The operation of the mind upon the sensations presented to it by the two eyes is exactly comparable to that which takes place when, on holding a marble between the finger and thumb, we at once declare it to be a single sphere (p. 439). That which is absolutely presented to the mind by the sense of touch in this case is by no means the sensa-

tion of one spheroidal body, but two distinct sensations of two convex surfaces. That these two distinct convexities belong to one sphere, is an act of judgment, or process of unconscious reasoning, based upon many particulars of past and present experience, of which we have, at the moment, no distinct consciousness.

LESSON XI

THE NERVOUS SYSTEM AND INNERVATION

1. The General Arrangement of the Nervous System.—The sensory organs are, as we have seen, the channels through which particular physical agents are enabled to excite the sensory nerves with which these organs are connected; and the activity of these nerves is evidenced by that of the central organ of the nervous system, which activity becomes manifest as a state of consciousness—the sensation.

We have also seen that the muscles are instruments by which a motor nerve, excited by the central organ with which it is connected, is able to produce motion.

The sensory nerves, the motor nerves, and the central organ, constitute the greater part of the *nervous system*, which, with its function of *innervation*, we must now study somewhat more closely, and as a whole.

The nervous apparatus consists of two sets of nerves and nerve-centres, which are intimately connected together and yet may be conveniently studied apart. These are the **cerebro-spinal** system and the **sympathetic** system. The former, or central nervous system, consists of the **brain** (see Fig. 1), including with this the **spinal bulb** or **medulla oblongata**, and **spinal cord** and the **cranial** and **spinal nerves**, which are connected with this axis. The latter comprises the chain of **sympathetic ganglia**, the nerves which they give off, and the various cords by which they are connected with one

another and with the cerebro-spinal nerves. (See Fig. 142.)

Nerves are made up entirely of **nerve-fibres**, the structure of which is somewhat different in the cerebro-spinal and in the sympathetic systems. (See p. 459.) Nerve centres, on the other hand, are composed of **nerve-cells** mingled with nerve-fibres. (See p. 466.) Such nerve-cells are found in various parts of the brain and spinal cord, in the sympathetic ganglia, and also in the ganglia belonging to spinal nerves as well as in certain sensory organs, such as the retina and the internal ear.

2. The Investing Membranes of the Cerebro-Spinal System.—The brain and spinal cord lie in the cavity of the skull and spinal column, the bony walls of which cavity are lined by a very tough fibrous membrane, serving as the periosteum of the component bones of this region, and called the **dura mater.** This is composed of a thick layer of densely interwoven fibres of connective tissue, with which a small amount of elastic tissue is mixed. The brain and spinal cord themselves are closely invested by a very *vascular* membrane of fibrous connective tissue, called **pia mater.** The numerous blood vessels supplying these organs run for some distance in the pia mater, and where they pass into the substance of the brain or cord, the fibrous tissue of the pia mater accompanies them to a greater or less depth.

Between the *pia mater*, and the *dura mater*, lies another delicate membrane, called the **arachnoid** membrane. These three membranes are connected with each other at various points, and the arachnoid, which is not only very delicate, but also less regular than the other two, divides the space between the dura and pia mater into two spaces, each containing fluid, and each more or less lined by a delicate epithelium. The space between the dura mater and the arachnoid, often called the **subdural space**, is nowhere very large ; but the space between the arachnoid and the pia mater, often called the **subarachnoid**

space, though small and insignificant in the region of the brain, becomes large in the region of the spinal cord, and here contains a considerable quantity of fluid, called **cerebro-spinal fluid.** This fluid has the appearance of ordinary lymph, but there the resemblance ends; for cerebro-spinal fluid contains only a minute amount of proteids (globulins), does not clot as true lymph does, and contains a peculiar reducing substance, which is, however, not a sugar.

3. The Arrangement and General Structure of the Spinal Cord and the Roots of the Spinal Nerves.—The spinal cord (Fig. 142) is a column of greyish-white soft substance, extending from the top of the spinal canal, where it is continuous by means of the spinal bulb with the brain, to about the second lumbar vertebra, where it tapers off into a filament. Starting at the level of the junction of the atlas vertebra with the skull, the spinal cord gives off laterally thirty-one pairs of **spinal nerves** whose trunks pass out of the spinal canal by apertures between the vertebræ, called the **intervertebral foramina**, and then divide and subdivide, their ultimate branches going for the most part to the muscles and to the skin. Each nerve originates from the cord by two roots, consequently there are twice as many roots as there are spinal nerves (Fig. 144). After their exit from the spinal canal the spinal nerves become connected with a chain of ganglia which lies parallel to the spinal cord and constitutes the sympathetic nervous system (Fig. 142), which will be described later on.

Transverse sections of the cord show that a deep, somewhat broad, fissure, the **anterior fissure** (Fig. 143, *1*), divides it in the middle line in front, nearly down to its centre: and a similar deeper but narrower cleft, the **posterior fissure** (Fig. 143, *2*), also extends nearly to its centre in the middle line behind. The pia mater extends more or less into each of these fissures, and supports the vessels which supply the cord with blood.

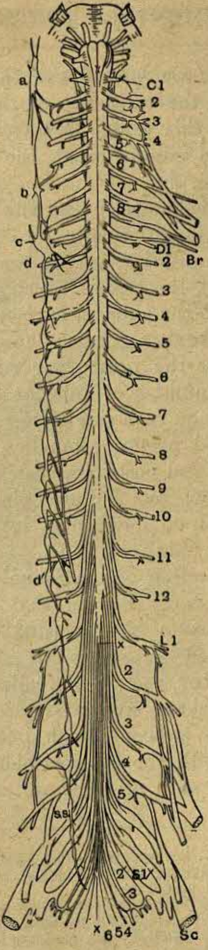


FIG. 142.—DIAGRAM, AS SEEN FROM THE FRONT, OF THE SPINAL CORD, THE SPINAL NERVES, AND ON ONE SIDE OF THE SYMPATHETIC CHAIN OF GANGLIA. (AFTER ALLEN THOMSON.)

The numbers of the thirty-one spinal nerves are shown on the right

In consequence of the presence of these fissures, only a narrow bridge of the substance of the cord connects its two halves, and this bridge is traversed throughout its entire length by a minute canal, the **central canal** of the cord (Fig. 143, *3*).

The lines of attachment of the roots of the spinal nerves divide the cord longitudinally into three parts, called respectively the anterior, lateral and posterior columns (Fig. 143, *8*, *7*, *6*), those roots which arise along the line which is nearer to the anterior surface of the cord being known as the **anterior roots**; those which arise along the other line are the **posterior roots** (Figs. 143 and 144). A certain number of anterior and posterior roots, on the same level on each side of the cord, converge and form anterior and posterior bundles, and then the two bundles, anterior and posterior, coalesce into the **trunk** of a spinal nerve; but before doing so, the posterior bundle presents an enlargement—**the ganglion of the posterior root** (Fig. 144, *Gn.*).

A transverse section of the spinal cord (Fig. 144, B, and Fig. 143), shows further that each half consists of two substances—a **white matter** on the outside, and a greyish-red substance in the interior. And this **grey matter,** as it is called, is so disposed that, in a transverse section, it looks, in each half, something like a crescent, with one end bigger than the other, and with the concave side turned outwards. The two ends of each crescent are called its **horns** or

half of the figure. *C*, 1-8, cervical; *D*, 1-12, thoracic (dorsal); *L*, 1-5, lumbar; *S*, 1-6, sacral; *Br*, brachial plexus; *Sc*, great sciatic nerve; *x*, terminal filament of spinal cord.

a, superior, *b*, middle, *c*, inferior cervical ganglion of the sympathetic system; of these *c* is fused with *d* the first thoracic (dorsal) ganglion. In some animals (dog and cat) the ganglion corresponding to *c*, the inferior cervical ganglion of man, is fused with the *upper three* thoracic ganglia into a common ganglion called the "stellate" ganglion (see Figs. 22, 23, *St.G.*) and the ganglion corresponding to *b*, the middle cervical ganglion of man, is in this case known as the inferior cervical ganglion. *d'*, the eleventh thoracic sympathetic ganglion; *l*, the first lumbar ganglion. The ganglia below *ss* are the sacral ganglia.

cornua, the one directed forwards being the **anterior cornu** (Fig. 143, *e e*); the one turned backwards the **posterior cornu** (Fig. 143, *a a*). The convex sides of

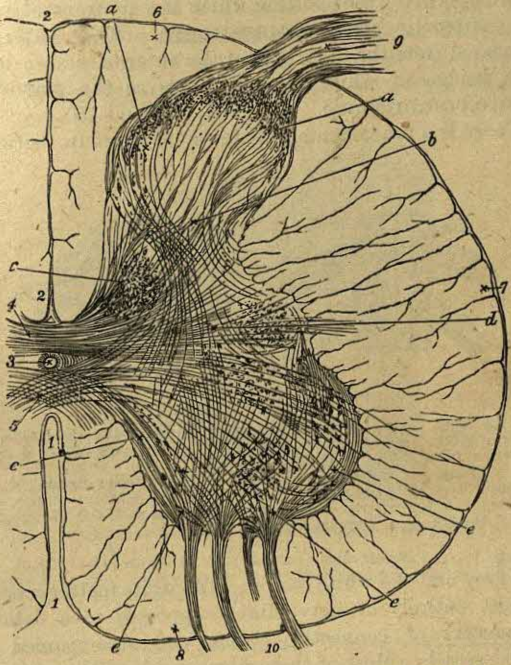


FIG. 143.—TRANSVERSE SECTION OF ONE-HALF OF THE SPINAL CORD (IN THE LUMBAR REGION), MAGNIFIED.

1, anterior fissure; 2, posterior fissure; 3, central canal; 4, and 5, bridges connecting the two halves (posterior and anterior commissures); 6, posterior column; 7, lateral column; 8, anterior column; 9, posterior root; 10, anterior root of nerve.

a a, posterior horn of grey matter; *e e e*, anterior horn of grey matter. Through the several columns 6, 7, and 8, each composed of white matter are seen the prolongations of the pia mater, which carry blood-vessels into the cord from the outside. The pia mater itself is seen over the whole of the cord.

the crescents of the grey matter approach one another, and are joined by the bridge which contains the central canal. The portion of this bridge which lies immediately behind the central canal is known as the **posterior grey commissure**; that portion which lies in front of it as the **anterior grey commissure.** The latter is separated from the inner end of the anterior fissure by a thin bridge of white matter known as the **anterior white commissure.** (See Figs. 143 and 150.)

There is a fundamental difference in structure between

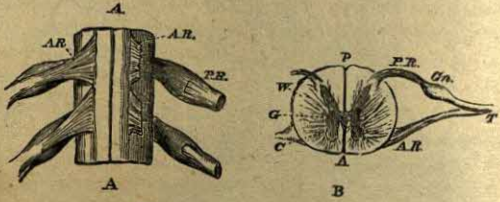


FIG. 144.—THE SPINAL CORD.

A. A front view of a portion of the cord. On the right side, the anterior roots, *A.R*, are entire; on the left side they are cut, to show the posterior roots, *P.R.*

B. A transverse section of the cord. *A*, the anterior fissure; *P*, the posterior fissure; *G*, the central canal; *C*, the grey matter; *W*, the white matter; *A.R.* the anterior root, *P.R.* the posterior root, *Gn.* the ganglion, and *T*, the trunk, of a spinal nerve.

the grey and the white matter. The white matter consists almost entirely of nerve-fibres supported in a delicate framework of connective tissue, and accompanied by blood-vessels. Most of these fibres run lengthways in the cord, and consequently, in a transverse section, the white matter is really composed of a multitude of the cut ends of these fibres.

The grey matter, on the other hand, contains in addition a number of nerve cells, some of them of considerable size. These cells are wholly, or almost wholly, absent in the white matter.

Many of the nerve-fibres of which the anterior roots are composed may be traced into the anterior cornu, and, indeed, into the nerve-cells lying in the cornu, while those of the posterior roots, for the most part, pass into this posterior column of white matter (Fig. 143, 6).

4. The Minute Structure of Medullated Nerves.—The white matter of the spinal cord consists chiefly of nerve-fibres; we may therefore, with advantage, consider

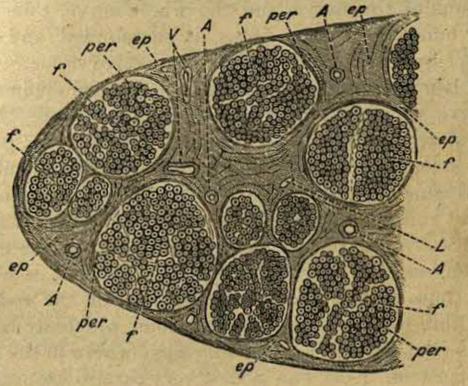


FIG. 145.—TRANSVERSE SECTION OF A MEDIUM-SIZED MEDULLATED NERVE.

ep, *ep*, general connective tissue sheath or epineurium; *f*, *f*, *f*, bundles of nerve-fibres bound together by the perineurium *per*, *per*, *per*; *A*, *A*, *V*, blood-vessels; *L*, lymphatic vessel.

the structure of these nerve-fibres before dealing in detail with the minute structure of the cord itself.

If a small piece of a nerve, which may be easily obtained from the leg of a freshly killed frog or rabbit, be teased out with needles on a glass slide and examined under a microscope it is seen to be made up chiefly of minute fibres. When the nerve has been suitably hardened it becomes possible to cut a transverse section of it; if this section be similarly examined the cut ends of the fibres

may be readily seen as little circular dots arranged in groups which compose the larger part of the section. These fibres are bound together in bundles, which are rounded as seen in section, by an external sheath or case of connective tissue called the **perineurium**, from whose inner surface very delicate layers of connective tissue pass in between the fibres of which each bundle is composed. The several bundles are themselves bound together by connective tissue to form the trunk of the nerve, and the whole nerve, thus built up of bundles of nerve-fibres, is surrounded and held together by an external layer of connective tissue.

The **nerve-fibres**, which are the essential elements of the nerve, vary in diameter from 2μ to 12μ or more. In the living state they are very soft cylindrical rods of a glassy, rather strongly refracting aspect. No limiting membrane is distinguishable from the rest of the substance of the rod, but running through the centre of it a band of somewhat less transparency than the rest may be discerned. At intervals, the length of which varies, but is always many times greater than the thickness of the rod, the nerve fibre presents sharp constrictions, which are termed **nodes** (Fig. 146, A, *n*; B. *n n*). Somewhere in the interspace between every two nodes, very careful examination will reveal the existence of a **nucleus** (Fig. 146, B. *n c*), invested by more or less protoplasmic substance and lying in the substance of the rod, but close to the surface.

As the fibre dies, and especially if it is treated with certain re-agents, these appearances rapidly change. 1. The outermost layer of the fibre becomes recognisable as a definite membrane, the **neurilemma**[1] (the so-called

[1] This word was formerly used to denote the whole nerve-case, now called *perineurium*; but its similarity to the word *sarcolemma* led to great confusion in the minds of students. It is undoubtedly a wholesome rule never to use an old word in a new sense; but the striking similarity between the two words "neurilemma" and "sarcolemma," and between the nerve-fibre sheath and the muscle-fibre sheath, seems an adequate excuse for an exception to the rule.

"primitive sheath" or "sheath of Schwann"). 2. The central band becomes more opaque, and sometimes appears marked with fine longitudinal striæ as if it were composed of extremely fine fibrillæ; it is the **neuraxon** or **axis-cylinder**. 3. Where the axis-cylinder traverses one of the nodes the neurilemma is seen to embrace it closely, but in the intervals between the nodes a curdy-looking matter, which looks white by reflected light, occupies the space between the *neurilemma* and the **axis-cylinder**. This is the **medulla** (the "white substance of Schwann") largely composed of a complex fatty substance often spoken of as *myelin*. If the neurilemma of a fresh fibre is torn, the myelin flows out and forms irregular lumps as if it were viscous. The medulla sometimes breaks, by oblique lines (Fig. 146, C. *m′*), extending from the axis-cylinder to the neurilemma, into segments, the faces of which are obliquely truncated and fit closely against one another. These may be seen even in quite fresh and living nerve-fibres. 4. The internodal nucleus is more sharply defined; and it will be seen to be attached to the inner surface of the neurilemma.

The essential part of each fibre, regarded as an instrument for the transmission of that molecular disturbance which is spoken of as a "nervous impulse," is the axis-cylinder. This is suggested by the fact that the axis-cylinder alone is apparently continuous throughout each fibre, since it passes across each node; but all doubt is removed when we find that the axis-cylinder alone provides the actual connection between the central nervous system and the distant structures to or from which the motor (efferent) or sensory (afferent) nerves run. Thus, if we follow along the course of a motor nerve, proceeding to its muscle, we find that it enters the perimysium (with which the superficial layer of the perineurium becomes continuous), and divides in the perimysial septa into smaller and smaller branches, each of which

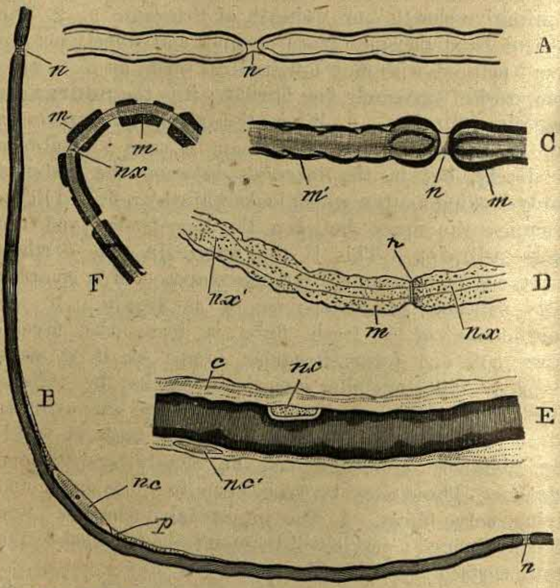


FIG. 146.—TO ILLUSTRATE THE STRUCTURE OF NERVE-FIBRES.

A. A nerve-fibre seen without the use of reagents, showing the "double contour" due to the medulla, and *n*, a node. Neither axis-cylinder nor neurilemma can be distinctly seen. (Magnified about 300 diameters.)

B. A thin nerve-fibre treated with osmic acid, showing, *nc*, nucleus with protoplasm, *p*, surrounding it, beneath the neurilemma; *n n*, the two nodes marking out the segment to which the nucleus belongs. (Magnified 400 diameters.)

C. Portion of fibre (thicker than B), treated with osmic acid to show the node *n*; *m*, the densely stained medulla; at *m'* the medulla is seen divided into segments. (Magnified 350 diameters.)

D. Portion of nerve-fibre treated to show the passage of the axis-cylinder, *nx*, through the node, *n*; *m*, the medulla. At *nx'* the axis-cylinder is swollen by the reagents employed and large and irregular. (Magnified 300 diameters.)

E. Portion of nerve-fibre treated with osmic acid, showing the nucleus, *nc*, embedded in the medulla; *c*, fine perineurial sheath lying outside the neurilemma; the outline of the latter can only be recognised over the nucleus *nc*; the nucleus, *nc'*, belongs to this perineurial sheath. (Magnified 400 diameters.)

F. Portion of nerve-fibre deprived of its neurilemma and showing the medulla broken up into separate fragments, *m m*, surrounding the axis-cylinder, *nx*.

contains the continuation of a certain number of the fibres of the nerve trunk, bound up into a bundle by themselves. In these larger ramifications of the nerve trunk there is no branching of the nerve fibres themselves (at any rate as a rule), but merely a separation of the fibres of the compound nerve bundles. In the finer branches, however, the nerve fibres themselves may divide; the division, *which always takes place at a node*, is generally dichotomous—that is, one fibre divides into two, each of these again into two, and so on. An ultimate branch consisting of one or two nerve fibres, or of one only, with a very delicate connective tissue envelope (Fig. 146, E *c*), passes to some single muscle fibre, and each nerve fibre applies itself to the outer surface of the sarcolemma. At this point, if it has not done so before, *the medulla disappears*, the neurilemma becomes continuous with the sarcolemma, and the *axis-cylinder* ending abruptly is applied to a disc of protoplasmic substance containing many nuclei, thus forming what is called a **motor end-organ** or **end-plate**,[1] which is interposed between the striated muscle substance and the sarcolemma at this point. Before ending the axis-cylinder divides and its divisions anastomose freely, but the exact relations of the various parts of the end-plate to the muscle-substance have not yet been clearly made out. The whole appears, however, to constitute an apparatus by which the molecular disturbances of the substance of the axis-cylinder (the essential part of the nerve) may be efficiently propagated to the substance of the muscle.

If, instead of following the motor nerve to its distribution in the muscle, we trace it the other way, towards the spinal cord, we shall find no alteration of any moment until we arrive at the point at which the anterior root enters the cord. From the finest branches of the motor nerve (in which, as has been stated, the nerve-fibres

[1] This is the arrangement in most vertebrated animals. In the frog the axis-cylinder branches out without entering a distinct motor end-plate.

themselves divide) to this point of entry each nerve-fibre extends ensheathed as *one continuous undivided axis-cylinder* in a long succession of internodal segments. At the point of entry into the cord the perineurium passes into the pia mater and the general connective tissue framework of the cord. The *neurilemma and the nodes disappear*. Often the axis-cylinder can be traced towards the anterior horn of the grey matter, invested only by a sheath of *medulla* which gradually becomes thinner and thinner until at length it *disappears*, and the fibre, thus reduced, passes into one of the processes of one of the large *nerve cells*, which lie in the anterior cornu of the grey matter (see p. 467).

The axis-cylinder of a motor nerve-fibre, therefore, is in fact an extremely fine and long process of a *nerve cell*, which passes at its peripheral end into one or more *muscle fibres*; in other words, the nerve cell and the muscle cells are the central and peripheral end-organs of the nerve-fibre.

With one or two exceptions, sensory (afferent) nerve-fibres are not distinguishable by any structural character from motor nerve-fibres. Wherever special-sense organules (p. 345) exist, the sensory fibres are connected with them by means of their axis-cylinder from which the neurilemma and medulla have disappeared. If, as before, we follow the sensory nerve-fibres back towards the spinal cord, we find that they pass through the ganglion on one of the posterior roots, and then enter the substance of the cord, passing towards the posterior cornu. Like the motor nerve-fibres, they lose their noded neurilemma as they enter the cord, so that in this case also it is again the axis-cylinder which provides the actually continuous connection between the sense organ and the central nervous system.

The neurilemma, with its nucleus, and the medulla may be regarded as a covering which provides for the protection and nourishment of each successive length of the essentially important axis-cylinder.

5. The Minute Structure of the Spinal Cord and Spinal Ganglia.—The spinal cord consists, as already described, of a central canal surrounded by grey matter composed largely of nerve-cells, and arranged in two crescent-shaped masses. The grey matter is surrounded by white matter, consisting chiefly of medullated nerve-fibres, and the whole is invested by the pia mater composed of connective tissue.

The pia mater carries the blood-vessels and lymphatics which supply the substance of the cord; it dips down into and completely fills the narrow so-called posterior fissure, and similarly lines the wider cavity of the anterior fissure. At frequent intervals, all over the surface of the cord, and in the fissures, the pia mater sends conspicuous prolongations (see Fig. 143) into the substance of the white matter, forming partitions or septa which run on the whole towards the grey matter, and thus carry the blood-vessels into the cord. These larger primary septa give off fine secondary septa, which still further subdivide the white matter, and provide for the more intimate distribution of minute blood-vessels throughout its substance. The inner ends of the septa are continued on into the grey matter for purposes similar to those which they subserve in the white matter.

The spaces in the white matter between the septa derived from the pia mater are filled by (i) medullated nerve-fibres, whose structure has been previously described, which run on the whole lengthwise or parallel to the long axis of the cord, and are supported by (ii) a fine felt-work of *extremely delicate* fibres, which constitutes what is known as the **neuroglia**, (*νεῦρον*=nerve, and *γλία*=glue) since it binds the nerve-fibres together. The fibres of the neuroglia are, in reality, processes from numberless minute cells, in which the body of each cell is extremely small, and the processes unusually numerous; these cells are known as neuroglia-cells (Fig. 147).

The processes of the neuroglia-cells are wrapped closely

round the nerve-fibres, and since they thus form a support and a covering for the fibres, the latter no longer need their natural external covering; or, in other words, the nerve-fibres of the white matter possess no neurilemma.

As in the white matter of the cord, so also in the grey matter, neuroglia occupies the spaces between the septa derived from the pia mater, and forms the supporting basis for the nervous constituents of the grey matter. The neuroglia is gathered into a specially well-marked layer immediately surrounding the central canal of the cord (Fig. 150, *c.g.s.*), and also, in a modified form, into a

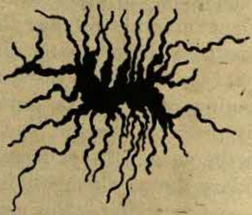


FIG. 147.—A NEUROGLIA-CELL FROM THE WHITE MATTER OF THE SPINAL CORD. (SCHÄFER.)

The body and processes of the cell appear black, since they were deeply stained in order to bring out their details.

conspicuous somewhat transparent mass at the outer end of the *posterior* horn of the grey matter, where it is known as the **substantia gelatinosa** of Rolando. (See Fig. 150, *sg.*).

The most striking feature of the grey matter is the presence in its neuroglia of nerve cells, many of which are very large and conspicuous, while others are smaller, but still very evident; the presence of these cells and of a closely interwoven network of non-medullated nerve-fibres, together with the *comparative* absence of medullated nerve-fibres, form the chief contrast between the structure of the grey and the white matter of the spinal cord.

The Cells of the Grey Matter.—These cells are not scattered uniformly throughout the grey matter, but arranged rather in groups. The largest cells occur in the outer end of the anterior horn (see Figs. 143 and 150), and since these are typical, as regards the main features of their structure, of all the cells of the grey matter, we may take one of them for detailed description.

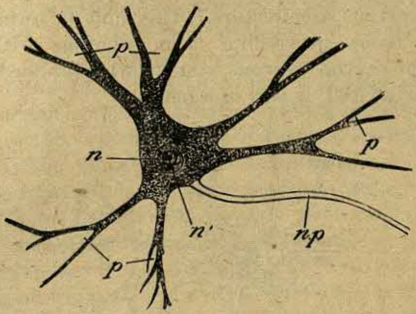


FIG. 148.—A LARGE NERVE CELL FROM THE ANTERIOR HORN OF THE SPINAL CORD.

n, Nucleus; *n'*, small body, called the nucleolus, inside the nucleus; *p*, branched processes or dendrites; *n.p*, unbranched axis-cylinder process or axon continued into the neuraxis of a motor nerve fibre.

The body of each cell is large (varying in diameter from 50μ to 100μ; $\frac{1}{500}$ to $\frac{1}{250}$ of an inch), and contains a very conspicuous nucleus (Fig. 148). The cell-body is prolonged into a varying number (usually many) of processes called dendrites dividing and subdividing into branches, which may be traced to some distance from the cell, becoming finer and finer, and finally ending abruptly. Besides these branching processes the cell bears one process, the axis-cylinder process, which does not divide in this way, passes straight away from the cell and is soon covered by a layer of myelin or a medulla; after its exit from the cord, it acquires additionally a neurilemma

or primitive sheath. In this way this process becomes the axis-cylinder of a medullated nerve-fibre, and is continuous to the organ, usually a muscle, to which it is distributed.

The fact is, the distinction between the so-called nerve-cell and the nerve-fibre is a wholly artificial one; these two, together with the nerve-ending, or a portion of it, being all constituent parts of one cell, which is the real unit of nervous architecture. This unit is termed the NEURON. Every nerve-fibre then, whether within or without the central nervous system, whether medullated or non-medullated, is part of a neuron.

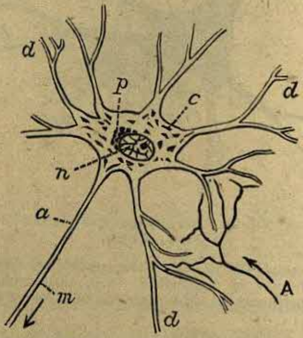


FIG. 149.—DIAGRAM OF A TYPICAL CELL FROM THE GREY MATTER OF THE SPINAL CORD. (SHERRINGTON.)

n, nucleus; *d*, *d*, *d*, branched processes (dendrites) from the cell-body; *p*, pigment; *c*, part of cell-body which stains very readily (chromatin); *a*, axis-cylinder process, which acquires first a medulla, *m*, and then (outside the cord) a neurilemma.

A, represents the processes (dendrites) from a neighbouring cell interlacing with, but not joined on to, the processes of the cell figured.

The other cells of the grey matter are generally similar in structure to the one described, though smaller than the cells of the anterior horn. Certain of them however exhibit particular features, on which we need not dwell here.

The rest of the grey matter, apart from the neuroglia, is made up of an interlacing network of naked (non-

medullated) axis cylinders ; but intermixed with these are a certain number of *very fine* medullated nerve-fibres, and a few large medullated fibres.

The Differences in Structure of the Spinal Cord at Various Levels.—These differences show themselves most conspicuously with respect to (i), the shape of the grey matter at various levels (ii), the position of the chief groups of nerve-cells in the grey matter, and (iii), the amount of white matter *relatively* to the grey matter at each level. The cord is widest in the cervical region, smallest in the thoracic (dorsal) region, and widens out again in the lumbar region. The chief structural differences to which we have alluded are very clearly indicated in Figure 150, which represents sections, drawn to scale, of (half) the spinal cord at the level of A the sixth thoracic (dorsal), B the sixth cervical, and C the third lumbar spinal nerves respectively.

The Structure of a Spinal Ganglion.—A spinal ganglion is, as we have said (Fig. 144, *Gn.*), an elongated swelling on the posterior roots of the spinal nerves. In a longitudinal section it is seen to consist of an external sheath of connective tissue which encloses groups of large nerve cells, of which the largest group lies at its outer side. The nerve fibres which enter the distal end of the ganglion on their way to the spinal cord pass in bundles in between the groups of nerve cells, and a certain amount of connective tissue with accompanying blood-vessels and lymphatics, also passes in amongst the nerve cells and nerve fibres. Each nerve cell (Fig. 151) consists like a nerve cell of the spinal cord, of a large nucleus, with a nucleolus, and of a cell body ; but the cell body is, in most cases at all events, prolonged into one process only, so that the whole cell is pear-shaped. This process soon acquires a medulla and a neurilemma ; it thus becomes an ordinary medullated nerve fibre, which then divides into two fibres, one of which may be traced into the nerve trunk, and the other along the posterior

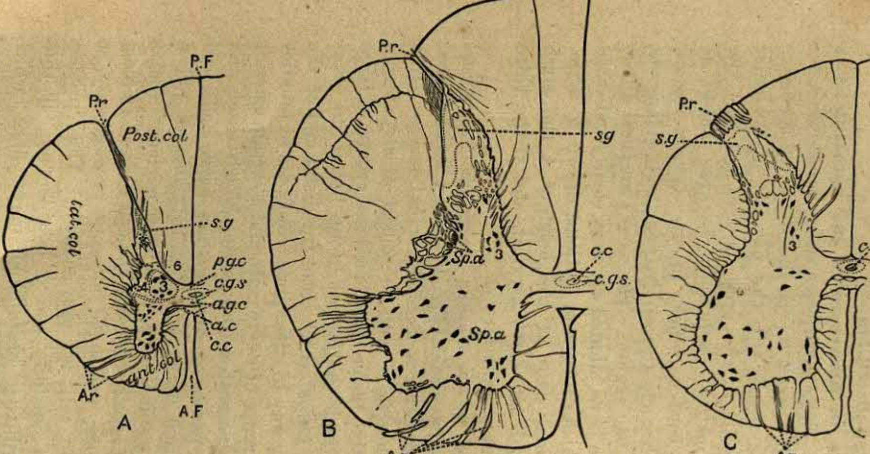


FIG. 150.—TRANSVERSE SECTIONS OF HALF THE SPINAL CORD, DRAWN TO SCALE, IN THE THORACIC (DORSAL), CERVICAL AND LUMBAR REGIONS. (AFTER SHERRINGTON.)

A, at the level of the sixth thoracic nerve; B, at the level of the sixth cervical nerve; C, at the level of the third lumbar nerve. *A.F.* anterior fissure; *P F.* posterior fissure; *ant.col.*, *lat.col.*, *post.col.*, anterior, lateral and posterior columns of the white matter; *Ar*, anterior roots; *Pr*, posterior root of spinal nerve; *c.c*, central canal; *a.c*, anterior white commissure; *a.g.c*, anterior grey commissure; *p.g.c.* posterior grey commissure; *s.g*, *substantia gelatinosa* of Rolando; *c.g.s*, gelatinous substance surrounding the central canal.

1. cells of the anterior horn; 3, group of cells known as the vesicular column or column of Clarke; 6, cells of the pos.erior horn.

root to the spinal cord. Hence the nerve-cells of the ganglion appear to be lateral appendages of the nerve-fibres, forming a junction with them after the fashion of a T-piece. On the central side of the ganglion the fibres continue their course into the substance of the spinal cord towards the posterior horn. Like the motor nerves they lose their neurilemma as they enter the cord. The majority of them turn aside as they enter the cord and run upwards in the posterior column of the cord

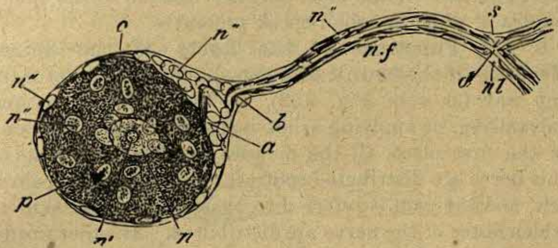


FIG. 151.—A NERVE CELL FROM THE GANGLION ON THE POSTERIOR ROOT OF A SPINAL NERVE.

The nerve cell, with *n*, nucleus, *n′*, nucleolus, *p*, protoplasmic body; *c*, capsule of the nerve cell; *n″*, nuclei of the capsule; *n.f.* the nerve fibre which, at the node, *d*, divides into two. At *a* the neuraxis of the fibre is lost in the substance of the cell; at *b* it acquires a medulla; at *n‴* nuclei are seen on the fibre. At the division the neuraxis *d* is seen to divide, and besides the neurilemma, *n.l.*, the fibre has an additional sheath, *s*, continuous with the capsule of the nerve cell.

to the brain. On their way thither the fibres give off numerous branches called collaterals; these are fine medullated fibres, they pass into the grey matter of the posterior horn and if their connections were traced they would lead for the most part to cells of the anterior horn or those of Clarke's column. They or their connections end in contact with these cells (A Fig. 150). Some of the posterior root fibres cross the cord and connect with neurons which ascend the opposite side. Therefore an impulse started in the skin would ultimately pass from the sensory neuron in either one or more of three directions: (1) To the sensory portion of the brain, (2) To

motor nerve, (3) to Clarke's column (Fig. 143), and thence to the cerebellum along the direct cerebellar tract (p. 491).

Structurally we may regard the nerve-fibres of the posterior roots of the spinal cord as taking their origin from one process of a cell in the spinal ganglion, in the same way that the fibres of the anterior root originate in one process of a nerve-cell in the anterior horn of the grey matter. This accounts for the peculiar way in which the fibres of the posterior root make their connection with the cord, and also for the most obvious function of the spinal ganglia of which we shall speak presently.

6. **The Functions of the Roots of the Spinal Nerves.**—If the **trunk** of a spinal nerve be irritated in any way (at x in Fig. 152), as by pinching, cutting, galvanising, or applying a hot body, two things happen: in the first place, all the muscles to which filaments of this nerve are distributed contract; in the second, pain is felt, and the pain is referred to that part of the skin to which fibres of the nerve are distributed. In other words, the effect of irritating the trunk of a nerve is the same as that of irritating its component fibres at their terminations.

The effects just described will follow upon irritation of any part of the *branches* of the nerve: except that when a branch is irritated, the only muscles directly affected, and the only region of the skin to which pain is referred, will be those to which that branch sends nerve-fibres. And these effects will follow upon irritation of any part of a nerve from its smallest branches up to the point of its trunk, at which the anterior and posterior bundles of root fibres unite.

If the *anterior bundle* of root fibres be irritated in the same way (at y, Fig. 152) only half the previous effects are brought about. That is to say, all the muscles to which the nerve is distributed contract, but no pain is felt.

So again, if the *posterior, ganglionated bundle* be irritated (at z, Fig. 152) only half the effects of irritating the whole trunk is produced. But it is the other half; that is to say, none of the muscles to which the nerve is distributed

contract, but pain is referred to the whole area of skin to which the fibres of the nerve are distributed.

It is clear enough, from these experiments, that all the power of causing muscular contraction which a spinal nerve possesses is lodged in the fibres which compose its anterior roots; and all the power of giving rise to sensation, in those of its posterior roots. Hence the anterior roots are commonly called *motor*, and the posterior *sensory*.

The same truth may be illustrated in other ways. Thus, if, in a living animal, the anterior roots of a spinal nerve be cut, the animal loses all control over the muscles to which that nerve is distributed, though the sensibility

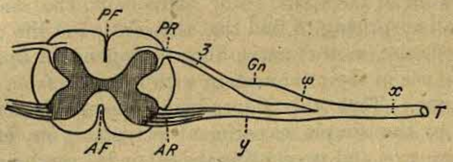


FIG. 152.—DIAGRAM TO ILLUSTRATE EXPERIMENTS IN PROOF OF THE FUNCTIONS OF THE SPINAL NERVE-ROOTS AND OF THE GANGLION ON THE POSTERIOR ROOT.

AF, anterior fissure of spinal cord; *PF*, posterior fissure; *AR*, anterior root of spinal nerve; *PR*, posterior root; *T*, trunk of spinal nerve; *Gn*, ganglion of posterior root.

of the region of the skin supplied by the nerve is perfect. If the posterior roots be cut, sensation is lost, and voluntary movement remains. But if both roots be cut, neither voluntary movement nor sensibility is any longer possessed by the part supplied by the nerve. The muscles are said to be paralysed; and the skin may be cut, or burnt, without any sensation being excited.

If, when both roots are cut, that end of the motor root which remains connected with the trunk of the nerve be irritated, the muscles contract; while, if the other end be so treated, no apparent effect results. On the other hand, if the end of the sensory root connected with the trunk of the nerve be irritated, no apparent effect is produced,

while, if the end connected with the cord be irritated, pain immediately follows.

When no apparent effect follows upon the irritation of any nerve, it is not probable that the molecules of the nerve remain unchanged. On the contrary, it would appear that the same change occurs in all cases; but a motor nerve is connected with nothing that can make that change apparent save a muscle, and a sensory nerve with nothing that can show an effect but the central nervous system.

We have already explained (p. 468) that a fibre of the anterior root of a spinal nerve is really part of a neuron the cell of which is situated in the anterior horn of the grey matter of the spinal cord. This being the case it is not at all surprising to find that the continued life of any of the efferent (motor) nerve-fibres is dependent upon the continuance of their connection with the cells from which they arise. That this dependence does really exist is shown by the simple experiment of cutting an efferent (motor) nerve, and preventing the cut ends from reuniting. When this is done it is found that shortly after the operation, those (peripheral) *parts of the nerve beyond the point of section*, i.e., *whose connection with the cells of the spinal cord has been cut off*, undergo what is called a "degeneration." This degeneration shows itself by structural changes in the nerve fibres. The medulla breaks up into oily drops, the axis cylinder also breaks into pieces and the neuclei of the neurilemma increase in number, together with an increase in the amount of granular protoplasm, which lies near them. The fragments of the medulla are next largely absorbed and disappear, and their place is taken by the protoplasm and nuclei derived from the neurilemma. While these structural changes are taking place, and even before they become obvious, the irritability of the nerve becomes gradually less, so that soon the nerve makes no response to any stimulus which may be applied to it. But the changes we have described do not occur in that (central)

part of the nerve which is still connected with the cells of the spinal cord; this part does not degenerate in the same way. Thus if the anterior efferent (motor) root of one of the spinal nerves be cut at *y* (Fig. 152), all the fibres of that root beyond *y* towards and along the trunk of the nerve *T* degenerate, while the portion of the root between *y* and the spinal cord does not degenerate.

If, now, we apply the same method of experiment to a posterior root the following results are observed. When the root is cut at *w* (Fig. 152), the fibres of that root towards and along the trunk of the nerve *T* degenerate; the central parts connected with the ganglion do not. If, on the other hand, the posterior root is cut at *z*, then the part of the root which lies between *z* and the spinal cord degenerates and the degeneration may be traced as far as the cut axis-cylinders penetrate into the central nervous system, whereas the portion still connected with the ganglion does not. Evidently, then, the life of the fibres in the posterior root is dependent upon their continued connection with the ganglion of that root, that is to say with the cells of that ganglion, of which the fibres are processes, as we have previously explained. These facts lead to the inevitable conclusion that the ganglion on the posterior root is the structure upon which the proper nutrition of the afferent fibres depends, or, in other words, the one clear and definitely ascertained function of the ganglion is to provide for the nutrition of these efferent nerve fibres which originate from the processes of the nerve cells in the ganglion.

This method of determining and localising the nutritional centres from which nerve-fibres grow is known as the "degeneration method,"[1] and has proved to be most helpful in determining the various "tracts," or paths in the spinal cord (and brain) along which nervous impulses of various kinds pass; with these we shall have to deal later on (see p. 489).

[1] Also as the "Wallerian method," after the name of the physiologist who first employed it.

7. The Physiological Properties of a Nerve.—It will be observed that in all the experiments described in the first part of the preceding section there is evidence that, when a nerve is irritated, a something which is spoken of as a **nervous impulse** and consists, probably, of a change in the arrangement or condition of its molecules, is propagated along the nerve-fibres. If a motor or a sensory nerve be irritated at any point, contraction in the muscle, or sensation, (or some other corresponding event) in the central organ, immediately follows. But if the nerve be cut, or even tightly tied at any point between the part irritated and the muscle or central organ, the effect at once ceases, just as cutting a telegraph wire stops the transmission of the electric current or impulse. When a limb, as we say, "goes to sleep," it is frequently because the nerves supplying it have been subjected to pressure sufficient to interfere with the nervous conductivity of the fibres, that is their power to transmit nervous impulses. We lose voluntary control over, and sensation in, the limb, and these powers are only gradually restored as that nervous conductivity returns.

Having arrived at this notion of an impulse travelling along a nerve, we readily pass to the conception of a sensory nerve as a nerve which, when active, brings an impulse to the central organ, or is *afferent;* and of a motor nerve, as a nerve which carries away an impulse from the organ, or is *efferent.* It is very convenient to use these terms to denote the two great classes of nerves; for, as we shall find (p. 483), there are afferent nerves which are not sensory in the sense of giving rise to a change of consciousness, or sensation, while there are efferent nerves which are not motor, in the sense of inducing muscular contraction. The nerves, for example, by which the electrical fishes give rise to discharges of electricity from peculiar organs to which those nerves are distributed, are efferent, inasmuch as they carry impulses to the electric organs, but are not motor, inasmuch as

they do not give rise to movements. The pneumogastric when it stops the beat of the heart cannot be called a motor nerve, and yet is then acting as an efferent nerve. Similarly the nerves which cause the cells of a gland such as the salivary glands, sweat glands, &c., to commence secreting are not motor nerves but are strictly efferent as regards the direction in which they convey their impulses. It will, of course, be understood, as pointed out above, that the use of these words does not imply that when a nerve is irritated in the middle of its length, the impulses set up by that irritation travel only away from the central organ if the nerve be efferent, and towards it, if it be afferent. On the contrary, we have evidence that in both cases the impulses travel both ways. All that is meant is this, that the afferent nerve from the disposition of its two ends, in the skin, or other peripheral organs on the one hand, and in the central organ on the other, is of use only when impulses are travelling along it towards the central organ, and similarly the efferent nerve is of use only when impulses are travelling along it, away from the central organ.

There is no difference in structure, in chemical or in physical character, between afferent and efferent nerves. The impulse which travels along them requires a certain time for its propagation, and is vastly slower than many other movements—even slower than sound. (See p. 481.)

We know but little of the nature of a nervous impulse. We know that it may be started in a nerve by various artificial means such as by pinching or knocking the nerve, or by suddenly warming or cooling it, and, most readily, by stimulating the nerve electrically. And we suppose that by any of these means there is set up in that bit of nerve to which any one of the above "stimuli" is applied, a disturbance, which is then propagated in succession from one particle (or molecule) of the axis cylinder to the next, so that it ultimately reaches a point in the nerve remote from that in which it was started. In this

way we come to speak of a nervous impulse as due to the propagation of a "molecular disturbance" along a nerve. But this expression serves rather to hide our ignorance than to explain what the impulse really is.

Electrical Properties of a Nerve.—In the case of a muscle we saw (p. 300) that its entry into a state of (contracting) activity was accompanied by an easily recognised change of shape, by chemical changes and by changes of temperature. Of these the first is of course entirely wanting in a nerve when it becomes active, *i.e.* is conveying an impulse, and the other two kinds of change have not so far been shown to take place in a nerve. But we saw also that the contracting activity of a muscle is accompanied by an electrical disturbance; a similar disturbance takes place in a nerve as the impulse sweeps along it, and is indeed the only evidence we possess of any change which accompanies the transmission of that impulse. Hence in a nerve this electrical phenomenon becomes of extreme interest and merits a short consideration.

If a piece of nerve, as for instance the sciatic nerve (see Fig. 90), from a freshly-decapitated frog, is removed from the body and suitably examined, it is found that *each cut end* of the nerve is *electrically negative* as compared with any other point of the nerve nearer to its middle or equator. Hence if one end B (Fig. 153), of the nerve and its middle point C are brought into contact with the terminals a,b, of a sensitive galvanometer[1] G, the needle of this instrument is at once deflected in a direction which shows that an electric current is passing (through the galvanometer) from the middle of the nerve to the cut end. If, now, when the needle has come to rest under the influence of this current, the end A of the nerve be stimulated at x, the needle of the galvanometer is seen to *swing back towards the position it occupied before it was deflected by the current from the nerve.* This means that as

[1] A galvanometer is an instrument used for the detection and measurement of electric currents.

the impulse which was started by the stimulus at x passes under the terminal b, that part of the nerve on which this terminal rests, becomes momentarily less electrically positive, that is to say *becomes electrically negative as compared with its condition before the passage of the impulse.* This statement holds equally good when the terminal b is applied to any other point of the nerve, either towards A or towards B, any difference in the result of stimulating the nerve at x being merely one of degree (as regards the extent to which the needle of the galvanometer moves), and not of kind (as to the direction in which the needle moves). Hence we may say without any possibility of

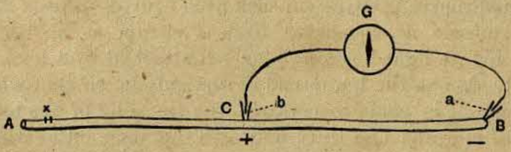


FIG. 153.—TO SHOW ARRANGEMENT OF A NERVE AND GALVANOMETER FOR EXPERIMENTS ON THE ELECTRICAL PROPERTIES OF A NERVE.

AB, a piece of nerve ; G, a galvanometer connected by wires and the electrodes a, b, with the end B and the middle point C of the nerve.

doubt that when an impulse travels along a nerve each point of the nerve becomes electrically negative as the impulse reaches that point ; and conversely we may use this electrical change in the nerve as unfailing evidence of the passage of an impulse along it. Apart from this electrical change we have no other means, such as exist in the case of a muscle, of determining when a nerve enters into a state of activity during the passage of an impulse.

The Rate of Transmission of a Nervous Impulse.—By means of a complicated arrangement of apparatus it is possible to determine very exactly the interval of time which elapses between the moment at which the stimulus is applied to the nerve at x (Fig. 153) and the instant at

which the needle of the galvanometer begins to move as the result of the passage of the impulse, started at x, under the terminal b at the point C. If now we measure the length of the piece of nerve between x and b we can at once calculate the rate at which the impulse travels along the nerve. Thus if the distance from x to b is 25 millimetres (1 inch), about ·00089 of a second elapses before the impulse started at x makes itself obvious as an electrical disturbance at b. That is to say the impulse travels at the rate of about 28 metres or 90 feet per second in the nerve of a frog.

The rate of transmission of an impulse along a (motor) nerve may also be determined in the following way, using a muscle nerve preparation such as is figured on page 298. The muscle is suspended from a clamp, as shown in Fig. 154; a light horizontal lever is attached by a hook to the tendon at the lower end of the muscle, so that when the muscle is made to contract the free end of the lever moves upwards and thus indicates the moment at which the contraction of the muscle commences. The sciatic nerve is then arranged in such a way that it may be stimulated either at a point x (Fig. 154) as close as possible to its junction with the muscle, or at a point y as far away as possible from the muscle. By the use of suitable apparatus it is easy to measure the interval of time which elapses between the moment of applying the stimulus at x and the moment at which the end of the lever begins to move. This is found to be, in an ordinary experiment, about $\frac{1}{100}$th of a second. If now the nerve is stimulated at y, it is found that the end of the lever begins to move slightly later than it did when the stimulus was applied at x; that is to say, the muscle begins to contract rather later when its nerve is stimulated at y than at x. This difference can only be due to the fact that *when the impulse is started at y it takes longer to reach the muscle than when it is started at x.* Since the length of the piece of nerve between y and x is known by direct measurement,

it becomes a simple matter to calculate the rate at which the impulse travels from y to x. The result thus obtained agrees quite closely with the one arrived at in the experiment previously described in which a galvanometer was used, namely 28 metres or 90 feet per second.

The rate at which an impulse travels along a nerve is closely dependent on the temperature of the nerve, and

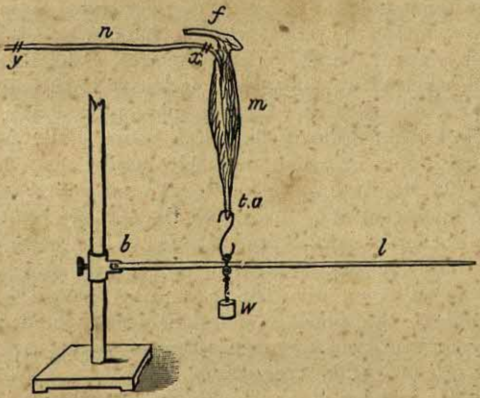


FIG. 154.—ARRANGEMENT OF NERVE, MUSCLE AND LEVER FOR DETERMINING THE VELOCITY OF A NERVOUS IMPULSE.

f, femur; *m*, muscle; *t.a*, tendon; *l*, lever, movable about the end *b*; *w*, weight to keep the muscle stretched; *n*, the nerve; *x* and *y*, the two points at which the nerve is stimulated

diminishes as the nerve is cooled; thus, by cooling a frog's nerve the rate may be reduced to as little as 1 metre (3 feet) per second. Hence it is not surprising that when experiments are made on the nerves of a warm-blooded human being, the rate of transmission is found to be somewhat greater, viz., about 100 metres (or over 300 feet) per second, than in the cold-blooded frog.

The most efficient stimulus which can be *artificially*

applied to a nerve for starting an impulse along it, is, as we have said (p. 477), an electrical stimulation. Further, as we have seen, each point of the nerve undergoes an electrical change, as the impulse reaches that point. These two facts frequently give rise to the entirely erroneous idea that a nervous impulse is of the nature of an electric current, similar to that which passes along a wire, as used for telegraphy. But this is by no means the case, since, without going into any other more abstruse reasons, we have shown that the rate at which an impulse travels along a nerve is on an average about 100 metres, or 300 feet, per second, whereas we know that electricity travels along a wire at a rate such that the transmission of signals over the wires of an ordinary hand-line is practically instantaneous. Even in one of the cables across the Atlantic Ocean (2,500 miles in length) only two-tenths of a second elapse after contact is made with the battery at one end before the effect can be first detected at the other end. Now, if a nerve could be used for transmitting an impulse as a signal from, say, Land's End to John o'Groat's (600 miles), the signal would take nearly three hours (176 minutes) to reach its destination, travelling as it does at the rate of 300 feet per second. We have spoken of a nervous impulse as a "molecular disturbance" propagated along a nerve. And if we may illustrate what is meant by this expression, by likening the process of the transmission of a nervous impulse to the transmission of any other condition with which most people are familiar, we might compare it with the passage of the explosion along a train of gunpowder when a spark is applied to one end of it. In this case the spark merely sets up a molecular change or disturbance in the grains of powder to which it is applied; the change thus set up leads to a similar change in the next neighbouring grains and so on along the whole train of powder, so that ultimately the result of applying the spark *at one end* makes its appearance as a similar result *at the other end* of the train.

Similarly in a nerve we may regard the stimulus as setting up a change, whose nature we do not as yet understand, at the point to which it is applied; this change sets up a similar change in the next neighbouring particles of the nerve, and so on until it finally appears at the furthest end of the nerve. But a nerve, unlike the train of gunpowder, relays itself so long as it is alive, as soon as the impulse has passed along it, whereas the train of powder is "dead" after the passage of the explosion, and must be artificially relaid for further use.

8. The Properties or Functions of the Spinal Cord.—Up to this point our experiments have been confined to the nerves. We may now test the properties of the spinal cord in a similar way. If the cord be cut across (say in the middle of the back), the legs and all the parts supplied by nerves which come off below the section, will be *insensible*, and *no effort of the will can make them move*; while all the parts above the section will retain their ordinary powers.

When a man hurts his back by an accident, the cord is not unfrequently so damaged as to be virtually cut in two, and then *insensibility* and *paralysis* of the lower part of the body ensue.

If, when the cord is cut across in an animal the cut end of the portion below the division, or away from the brain, be irritated, violent *movements* of all the muscles supplied by nerves given off from the lower part of the cord take place, but *no sensation* is felt by the brain. On the other hand, if that part of the cord, which is still connected with the brain, or better, if any afferent nerve connected with that part of the cord be irritated, *sensations ensue*, as is shown by the movements of the animal; but in these movements the *muscles* supplied by the nerves coming from the spinal cord below the cut *take no part*: they remain perfectly quiet.

Thus, it may be said that, in relation to the brain the

cord is a great mixed motor and sensory nerve. But it is also much more.

Reflex Action through the Spinal Cord.—If the trunk of a spinal nerve be cut through, so as to sever its connection with the cord, an irritation of the skin to which the sensory fibres of that nerve are distributed produces neither motor nor sensory effect. But if the cord be cut through anywhere so as to sever its connection with the brain, irritation applied to the skin of the parts supplied with sensory nerves from the part of the cord *below the section*, though it gives rise to no sensation, may produce violent motion of the parts supplied with motor nerves from the same part of the cord.

Thus, in the case supposed above, of a man whose legs are paralysed and insensible from spinal injury, tickling the soles of the feet will cause the legs to kick out convulsively. And as a broad fact, it may be said that, so long as both roots of the spinal nerves remain connected with the cord, irritation of any afferent nerve is competent to give rise to excitement of some, or the whole, of the efferent nerves so connected.

If the cord be cut across a second time at any distance below the first section, the efferent nerves below the second cut will no longer be affected by irritation of the afferent nerves above it—but only of those below the second section. Or, in other words, in order that an afferent impulse may be converted into an efferent one by the spinal cord, the afferent nerve must be in definite material communication with the efferent nerve, by means of a neuron in the spinal cord. The nature of these communications we have already seen (p. 472).

This peculiar power of the cord, by which it is competent to convert afferent into efferent impulses, is that which distinguishes it physiologically, as a central organ, from a nerve, and is called **reflex action.** It is a power possessed by the grey matter, and not by the white substance of the cord.

The number of the efferent nerves which may be

excited by the reflex action of the cord, is not regulated alone by the number of the afferent nerves which are stimulated by the irritation which gives rise to the reflex action. Nor does a simple excitation of the afferent nerve by any means necessarily imply a corresponding simplicity in the arrangement and succession of the reflected motor impulses. Tickling the sole of the foot is a very simple excitation of the afferent fibres of its nerves; but in order to produce the muscular actions by which the legs are drawn up, a great multitude of efferent fibres must act in regulated combination. In fact, in a multitude of cases a reflex action is to be regarded rather as the result of a dormant activity of the spinal cord awakened by the arrival of the afferent impulse, as a sort of orderly explosion fired off by the afferent impulse, than as a mere rebound of the afferent impulse into the first efferent channels open to it.

The various characters of these reflex actions may be very conveniently studied in the frog. If a frog be *decapitated*, or, better still, if the spinal cord be divided close to the head, and the brain be destroyed by passing a blunt wire into the cavity of the skull, the animal is thus deprived (by an operation which, being almost instantaneous, can give rise to very little pain) of all consciousness and volition, and yet the spinal cord is left intact. At first the animal is quite flaccid and apparently dead, no movement of any part of the body (except the beating of the heart) being visible. This condition, however, being the result merely of the so-called shock of the operation, very soon passes off, and then the following facts may be observed.

So long as the animal is untouched, so long as no stimulus is brought to bear upon it, no movement of any kind takes place: *volition is wholly absent.*

If, however, one of the toes be gently pinched, the leg is immediately drawn up close to the body.

If the skin between the thighs around the anus be

pinched, the legs are suddenly drawn up and thrust out again violently.

If the flank be very gently stroked, there is simply a twitching movement of the muscles underneath; if it be more roughly touched, or pinched, these twitching movements become more general along the whole side of the creature, and extend to the other side, to the hind legs, and even to the front legs.

If the digits of the front limbs be touched, these will be drawn close under the body as in the act of clasping.

If a drop of vinegar or any acid be placed on the top of one thigh, rapid and active movements will take place in the leg. The foot will be seen distinctly trying to rub off the drop of acid from the thigh. And what is still more striking, if the leg be held tight and so prevented from moving, the other leg will begin to rub off the acid. Sometimes if the drop be too large or too strong, both legs begin at once, and then frequently the movements spread from the legs all over the body, and the whole animal is thrown into convulsions.

Now all these various movements, even the feeblest and simplest, require a certain combination of muscles, and some of them, such as the act of rubbing off the acid, are in the highest degree complex. In all of them, too, a certain purpose or end is evident, which is generally either to remove the body, or part of the body, from the stimulus, from the cause of irritation, or to thrust away the offending object from the body: in the more complex movements such a purpose is strikingly apparent.

It seems, in fact, that in the frog's spinal cord there are sets of nervous machinery destined to be used for a variety of movements, and that a stimulus passing along a sensory nerve to the cord sets one or the other of these pieces of machinery at work.

Thus one important function of the spinal cord is to serve as an independent nervous centre, capable of originating combined movements upon the reception of the

impulse of an afferent nerve, or rather, perhaps, a group of such independent nervous centres.

In all these reflex actions of the spinal cord, the structures necessary for their performance are, as already pointed out (p. 340), a sensory surface, an afferent nerve, a portion of the grey matter of the cord, an efferent nerve, and a muscle or group of muscles. In the case of the headless frog, the actions are of course quite involuntary, and performed unconsciously, and the same remark holds good in the case of a man whose spinal cord is so injured as to be practically cut in two. But even in an uninjured healthy man, similar reflex actions, although now under the control of the will, are strikingly manifest, and play an important part in his everyday life. Thus the act of walking, though started by the will, is subsequently a reflex action. When engaged in conversation or buried in thought, a person walks with all his ordinary dexterity, but in entire unconsciousness of the action. In this case the afferent impulses are largely started from the stimulation of the skin of the feet and legs which results from the varying pressure and contact with the ground. Hence the staggering gait in cases where, as a result of disease, the chain of structures requisite for the liberation of the reflexes is broken, as for instance by disease of the posterior (afferent) roots of the spinal nerves. In such cases walking is frequently possible only as the result of *looking* at the ground (see p. 390); this accords with the fact that even in health afferent impulses started in the sensory surface (retina) of the eye play an important part in giving rise to the reflexes of walking. But, on the other hand, blind persons walk with no little dexterity.

Again, the actions of micturition and defæcation are really reflex actions carried out by the spinal cord, as soon as they have been started by the will; here the sensory surfaces are the mucous membrane of the bladder or rectum, the necessary stimulus being supplied as the result of their distension by the accumulated urine or fæces.

Using the expression reflex action in a rather wider and more general sense we may here again draw attention to the importance of these actions to the working and welfare of the body as regards the relationships of its internal mechanisms. Thus we have seen that certain parts of the spinal bulb, or medulla, which for our present purpose may be regarded as part of the spinal cord, are connected with the heart (cardio-inhibitory centre), blood-vessels (vaso-motor centre), and respiratory muscles (respiratory centre) in such a way that impulses arising in outlying parts of the body, lead reflexly to such modified activity of each of the above systems, as may from time to time be necessary. (See pages 75, 70, 158).

Reflex action is a property of the central nervous system which is not confined to the spinal cord alone, or to the spinal bulb to which we have just extended it, but is also a marked characteristic of the varied activities of the brain. But to this point we shall return later on.

The Paths of Conduction of Afferent and Efferent Impulses along the Spinal cord. The spinal cord has a further most important function beyond reflex action, namely that of transmitting nervous impulses, as a great mixed motor and sensory nerve leading from the brain, between the brain and the various organs, such as the muscles and the skin, with which the spinal nerves are connected. When we move a foot, certain nervous impulses, starting in some part of the cerebral hemispheres, pass down along the whole length of the spinal cord as far as the roots of the spinal nerves going to the legs, and issuing along the fibres of the anterior bundles of these roots find their way to the muscles which move the foot. Similarly, when the sole of the foot is touched, afferent impulses travel in the reverse way upward along the spinal cord to the brain. And the question arises, in what manner do these efferent and afferent impulses travel along the spinal cord ?

We must now explain the method by which most of our present information has been obtained, and point out the chief and most definite facts which have been arrived at.

We have seen previously (p. 475) that when a nerve is cut, a structural change of its fibres starts at the cut. This is spoken of as a "degeneration," and since it indicates a breakdown in the proper nutrition of those fibres which are seen to degenerate may, as in the case of the roots of the spinal nerves, be used to determine the relationship of nerve fibres to the centres upon which their nutrition depends. The white matter of the spinal cord is composed of fibres which are in all essentials the same as those of an ordinary medullated nerve, and these fibres of the white matter may similarly degenerate when cut off from the centres on which their nutrition depends. Hence, if the whole spinal cord be cut across transversely, or if transverse cuts be made into any part, or the whole of any one or more of the columns of white matter of which the cord is so largely made up, degenerative changes may start from the point of section, and by the course they pursue up and down the cord, enable us to follow the course of certain fibres or bundles of fibres in that white matter. Now this is exactly what does happen when the cord is cut, and this "degeneration method" has provided the best means for answering the question as to how and along what paths afferent and efferent impulses travel up and down the spinal cord.

When the cord is cut across degenerative changes take place in parts of the white matter, both above and below the point of section. These changes only affect limited parts of the white matter, and the parts which are affected *above* the cut, that is up towards the brain, are different in position from the parts which are affected *below* the point of section. The changes which start from the cut and take place *upwards* along the spinal cord, towards the brain, are spoken of as **ascending** degenerations; those which are observed to occur *downwards* from below

the section, are known as **descending** degenerations, the terms ascending and descending being thus used to denote structural changes which start from the section and pass up towards or down from the brain respectively. Moreover, since the parts which degenerate are limited as to their transverse sectional area while running for very considerable distances along the white matter of the spinal cord, they are usually spoken of as "tracts," and since these tracts serve very definitely for the transmission of impulses up and down the cord, they denote very definite paths of conduction along the spinal cord.

Having thus explained the method of experimenting, we may now state the chief results obtained by its application.

(A). *Tracts of ascending degeneration.*

(i). **The Posterior Column comprising the Postero-median and Postero-lateral Tracts.**—These tracts occupy the posterior white columns of the spinal cord, adjacent to the posterior fissure, in each half of the cord. (Fig. 155, *p.m.*, *p.l.*).

The degeneration which marks out this tract follows not only upon sections of the cord itself, but more especially from cutting the posterior roots of the spinal nerves ; it is therefore the result of a severance of the fibres in this part of the cord from their nutritive centres in the cells of the ganglion on the posterior root. Hence it marks the course of fibres passing up the cord from the posterior roots, and denotes the path along which afferent (sensory) impulses travel up from the spinal nerves. Since these nerves are given off all along the cord, the tract is necessarily found to exist throughout the whole extent of the cord, and may be traced up into the spinal bulb, where it ends on the side up which it passes. The postero-median portion of the tract consists of fibres coming from the lower part of the body, the postero-lateral portion from the upper portion, hence the latter only exists in the upper part of the cord .

(ii). **The Direct Cerebellar Tract.**—This tract lies in

the outer and hinder part of the lateral columns (Fig. 155, *Cb.*, *Cb.*). The degeneration which marks its course results solely from sections of the cord itself, and not of any of the spinal nerve roots. It begins in the lower end of the cord at the level of the second lumbar nerve, passes straight up to the spinal bulb and then into the cerebellum by means of the *inferior peduncle* (see p. 506)

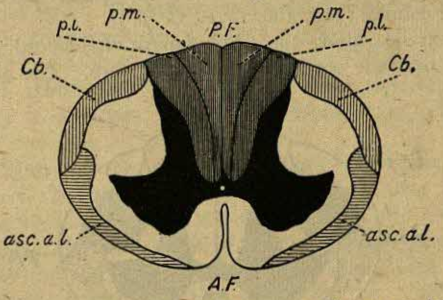


FIG. 155.—DIAGRAM TO SHOW THE POSITION OF TRACTS OF ASCENDING DEGENERATION IN THE WHITE MATTER OF THE SPINAL CORD AT THE LEVEL OF THE FIFTH CERVICAL NERVE.

A.F, anterior fissure; *P.F.* posterior fissure; *p.m.*, *p.l.* the median and lateral posterior tracts, or tract of fibres from the posterior roots of the spinal nerves; *Cb*, *Cb*, the cerebellar tract; *asc. a.l.*, *asc. a.l.* the ascending antero-lateral tract.

The grey matter of the cord is shaded black.

of this part of the brain. The fibres in this tract originate from processes of those cells in the grey matter which form a conspicuous group at the base of the dorsal horn, and are known as **Clarke's column.** These cells are seen most conspicuously in the thoracic, the upper cervical and the sacral regions of the cord. Those from the sacral region do not contribute to the Direct Cerebellar Tract. (See Fig. 150, 3).

(iii). **The Ascending Antero-lateral Tract.**—This tract, like the cerebellar, can only be made evident as the result of injury to the cord itself. Its fibres originate in the cells of Clarke's column in the lower portion of the spinal cord. It lies in the outer and anterior part of the

lateral column (Fig. 155, *asc. a.l.*, *asc. a.l.*) and commences rather lower down in the cord than does the cerebellar tract, but like the latter runs up to the spinal bulb, and enters the cerebellum by mean of its *superior peduncle.*

B. *Tracts of descending degeneration.*

(i) **The Crossed Pyramidal Tract.**—This is a large and conspicuous tract in the inner and hinder part of the lateral column (Fig. 156, *Cr.p.*, *Cr.'p.'*).

It extends along the whole length of the cord, passing down into the cord from the spinal bulb. The fibres of

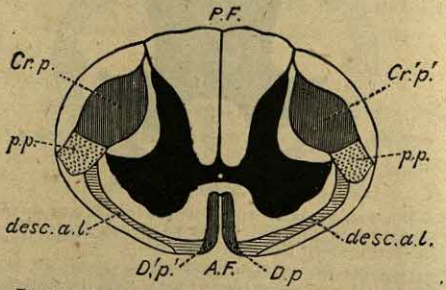


FIG. 156.—DIAGRAM TO SHOW THE POSITION OF TRACTS OF DESCENDING DEGENERATION IN THE WHITE MATTER OF THE SPINAL CORD AT THE SAME LEVEL AS IN FIG. 155.

Cr.p., *Cr'.p'.* crossed pyramidal tracts; *D'.p'.*, *D.p.* direct pyramidal tracts; *desc. a.l.*, *desc. a.l.* descending antero-lateral tract; *p.p*, *p.p.* pre-pyramidal tract.

this tract are believed to communicate with those cells in the anterior horns of the grey matter whose process, as previously described (p. 468), gives rise to the nerve fibres which leave the cord as the efferent (motor) anterior roots of the spinal nerves. The communication is made by a small neuron interposed between the two. It may thus be regarded as the path for efferent impulses coming down the cord on their way to outlying parts of the body.

But this tract, unlike those we have so far described, does not end, or rather we should now say begin, in the spinal bulb. On the contrary, it may be traced up through

the bulb into the higher parts of the brain and is found to start from a certain portion of what we shall describe later on as the **cortex of the cerebral hemispheres.** It is upon the cells of this part of the cortex that the fibres of the pyramidal tracts depend for their nutrition; hence injury to this portion of the cortex leads to a degeneration which extends right down to the lowest end of the spinal cord. These facts still further confirm the idea that this tract provides a path for efferent (motor) impulses in the cord, since, as we shall see, that part of the cerebral cortex of which we are now speaking, is specially concerned in the development of efferent (motor) impulses.

The fibres of this tract which enter the spinal bulb from, say, the **left** side of the brain, cross over in the bulb, in what is known as the *decussation of the pyramids* (p. 520) just above the origin of the first cervical nerve, and then pass down the **right** side of the spinal cord. For this reason it receives the name of the "crossed" pyramidal tract.

(ii) **The Direct Pyramidal Tract.**—This is a small tract in the median part of the anterior white columns, adjacent to the anterior fissure. (Fig. 156 *D′.p′.*, *D.p.*) It really consists of a small portion of those fibres which passed into the bulb as the main pyramidal tract coming from the cortex of the cerebral hemispheres, but which have *not yet crossed over* in the bulb. Instead of crossing in the brain they cross in the cord. Hence the tract grows small as it descends and ultimately disappears. Thus in Fig. 156 the direct tract *D.p.* comes from the same side of the brain as the crossed pyramidal tract *Cr.p.*, and a similar remark applies to *D′.p′.* and *Cr′.p′.*

(iii) **The Descending Antero-lateral Tract.**—This tract is not very clearly marked, in fact the fibres of the ascending and descending antero-lateral tract intermingle to some extent. It forms part of an alternative route from the cerebral cortex to the anterior horn cells. (Fig. 156, *desc.a.l.*, *desc.a.l.*)

(iv) **The Pre-pyramidal Tract.**—Like the descending tracts which we have already mentioned the pre-pyramidal tract ends in connection with the anterior horn cells. The impulses which its fibres carry come, however, not from the cerebrum but from the cerebellum. We have seen (p. 471) that a sensory impulse reaching the central nervous system by a fibre in the posterior root may expend itself either in the cerebrum, the cerebellum or the anterior horn; we now see that an anterior horn cell (motor neuron) may be played upon by impulses coming either from the cerebrum, the cerebellum or the sensory neurons of the posterior roots.

Such are the functions of the spinal cord, taken as a whole. The *spinal* nerves are, as we have said, chiefly distributed to the muscles and to the skin. But other nerves, such as those for instance belonging to the blood-vessels, the so-called *vaso-motor* nerves (Lesson II. p. 69), though many of them run for long distances in the sympathetic system, may ultimately be traced to the spinal cord. Along the spinal column the spinal nerves give off branches which run into and join the sympathetic system. And the vaso-motor fibres which run along in the sympathetic nerves do really spring from the spinal cord, finding their way into the sympathetic system through these communicating or commissural branches. Besides which, some vaso-motor fibres run in spinal nerves along their whole course.

Experiments, moreover, go to show that the nervous influences which, through these vaso-motor nerves, regulate the blood-vessels, now forcibly constricting them, now allowing them to dilate, and now keeping them in a state of moderate or tonic constriction, proceed from the spinal cord.

The cord is, therefore, spoken of as containing *centres* for the vaso-motor nerves or, more shortly, *vaso-motor centres*.

For example, the muscular walls of the blood-vessels

supplying the ear and the skin of the head generally, are made to contract, as has been already mentioned, by nervous fibres derived immediately from the sympathetic (Fig. 22, *C.Sy.*). These fibres are non-medullated and arise from cells situated in the superior cervical ganglion. The ganglion in turn is connected with the spinal cord by medullated fibres which do not arise from the sympathetic ganglia, but simply pass through them on their way from the upper dorsal region of the cord. Irritation of this region of the cord produces the same effect as irritation of the vaso-motor nerves themselves, and destruction of this part of the cord paralyses them.

It has, however, been further shown that the nervous influence does not originate here, but proceeds from higher up, from the medulla oblongata in fact, and simply passes down through this part of the spinal cord on its way to join the sympathetic nerves.

9. The Sympathetic Nervous System.—The sympathetic system consists chiefly of a double chain of ganglia lying at the sides and in front of the spinal column, and connected with one another, and with the spinal nerves, by commissural cords (Fig. 142). From these ganglia, nerves are given off which for the most part follow the distribution of the blood-vessels, but which, in the thorax and abdomen, form great networks, or *plexuses*, upon the heart and about the stomach and other abdominal viscera. Every efferent impulse which passes along the sympathetic system leaves the spinal cord by a medullated fibre—a portion of a neuron the cell of which is in the grey matter. This neuron ends in the sympathetic system (either in a ganglion or elsewhere) in connection with the cell of another neuron, non-medullated, which carries the impulse to the end organ. Some of these non-medullated fibres run back into the spinal nerves for distribution to the blood-vessels of the limbs.

By means of the sympathetic nerves the muscles of the vessels generally, and those of the heart, of the intestines,

and of some other viscera may, as we have seen, be influenced; and the influence thus conveyed, it may be remarked, is generally different to, or even antagonistic to that which is conveyed to the same organs by the fibres running in the spinal or cranial nerves. Thus while irritation of the (cranial) pneumogastric fibres stops the heart, irritation of the sympathetic fibres going to the heart increases the beat.

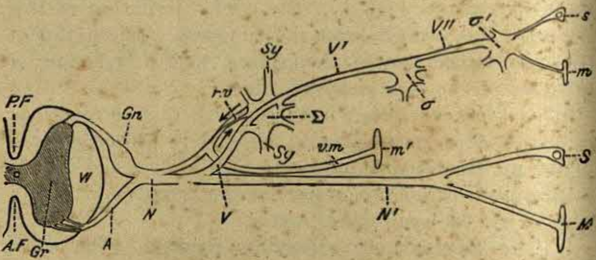


FIG. 157.—DIAGRAM TO ILLUSTRATE THE DISTRIBUTION OF THE SPINAL NERVES AND THEIR RELATIONSHIP TO THE GANGLIA OF THE SYMPATHETIC SYSTEM.

A.F, anterior fissure; *P.F*, posterior fissure; *Gr*, grey matter; *W*, white matter of spinal cord; *A*, anterior root of spinal nerve; *Gn*, ganglion on the posterior root; *N*, the trunk of a spinal nerve; *N′*, spinal nerve proper, ending in a skeletal muscle *M*, in a sensory cell or surface *S*; *V*, a branch (white ramus communicans) of the spinal nerve passing to Σ a ganglion of the sympathetic system, then passing on as *V′* to some more distant ganglion σ, and then as *V″* to some peripheral ganglion σ′, and ending in a muscle *m* of the blood-vessels or viscera, in *s* an internal (visceral) sensory cell or surface.

From Σ a nerve *r.v.* (grey ramus communicans) runs back and passes partly towards the spinal cord and partly to the periphery, as vaso-motor fibres and other *v.m.*, in connection with the spinal nerve *N′*, to *m* the muscles of blood-vessels in certain parts *e.g.* of the limbs.

Sy, *Sy*, the main chain of the sympathetic system which unites the several ganglia Σ of that system. (See Fig. 142.)

But the influences which thus reach these organs through the sympathetic nerves, do not originate in the sympathetic system itself, but are derived from the spinal cord or brain. We have seen (p. 69) this to be the case in reference to vaso-motor nerves, and the same is true of the sympathetic nerves going to the heart and other

viscera. Whatever may turn out to be the function of the sympathetic ganglia, there is at present no adequate evidence that they in any way act as nervous centres, either of reflex action, or of any other form of nervous activity. Hence the sympathetic is not to be regarded as a separate nervous system, but as being in reality merely an outlying part of the cerebro-spinal system, an outlying chain of ganglia, through which the fibres of a part of the trunk of each spinal nerve pass on their way to the viscera. This relationship is made quite clear by the accompanying diagram (Fig. 157).

We have spoken of the fibres which proceed from cells

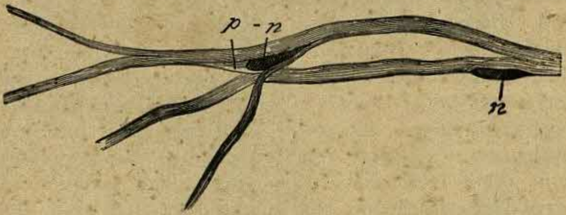


FIG. 158.—PALE NON-MEDULLATED FIBRES FROM THE PNEUMOGASTRIC NERVE. (RANVIER.)

n, nucleus; *p*, protoplasm belonging to the nucleus.

situated in the sympathetic system as *non-medullated*, because they possess no medulla. They appear under the microscope as pale flattened bands, about as wide as small medullated fibres, often fibrillated longitudinally, and frequently dividing. They appear, in fact, to be axis-cylinders, without medulla, and in cases perhaps without a neurilemma, though they bear at intervals on their surface nuclei which may represent the inter-nodal nuclei of ordinary nerve fibres.

The ganglia of the sympathetic system are composed of nerve cells bound together by a small amount of loose connective tissue. The cells differ somewhat in appearance and arrangement according to the ganglion in

which they are seen, but speaking broadly and generally they may be said to resemble in their most obvious features the motor cells of the spinal cord, whose structure we have previously described (p. 467). Like the latter, each nerve cell of a sympathetic ganglion contains a large and conspicuous nucleus, and the cell body is prolonged into a varying but usually large number of branching processes (dendrites). Moreover, each cell possesses one process which does not branch but passes away from the body of the cell as a (usually) *non-medullated* nerve fibre, to be distributed to the various tissues (p. 495) which it influences, and is in this respect similar to the axis-cylinder process of a cell of the spinal cord. Each ganglion is also connected with nerve fibres which come to it from the central nervous system (Fig. 157). These fibres mostly end in connections with the nerve cells. Sometimes a fibre does not end in the first ganglion it meets, but passes right through it into one of the nerves going off from that ganglion, and so reaches some other more distant ganglion. The number of nerve fibres which thus pass into the ganglion from the spinal cord is much less than the number of nerve cells in the ganglion; hence many more nerve fibres are found coming from the ganglion than entering it. By this arrangement each ganglion provides, as it were, a sort of junction by means of which any nervous impulses which reach it along any one path may be the more readily and widely distributed, along several paths, to the tissues.

10. **The Structural Arrangements of the Brain and Spinal Bulb (Medulla Oblongata).**—The brain is a very complex organ consisting of many parts. It occupies the cavity of the skull and is thus placed at the upper end of the spinal cord with which it becomes connected by means of the spinal bulb[1]; this passes insensibly into, and in its lower part has the same structure as, the spinal cord. When viewed from the side, after the removal of the parts

[1] Throughout this section we shall use the word "bulb" in shortness for spinal bulb, and instead of the older name "medulla oblongata."

which cover in the cerebro-spinal system, the brain presents the appearance shown in the following figure. The spinal cord (*N*) widens out into the bulb (*M.Ob.*) whose

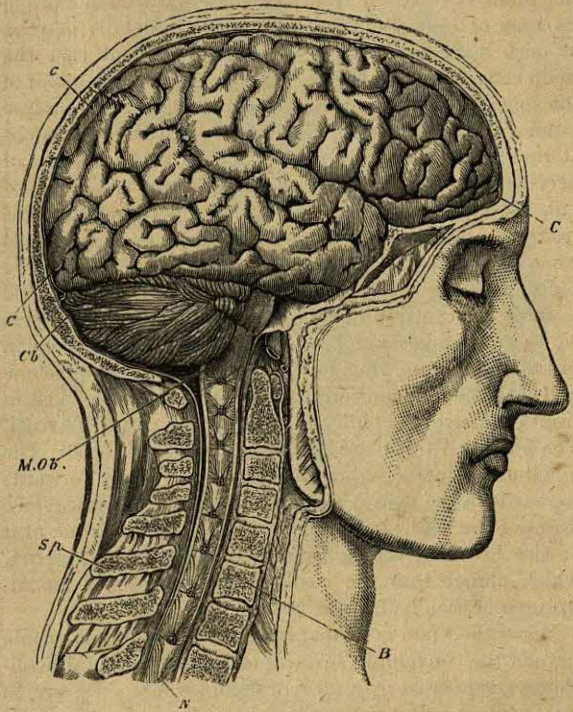


FIG. 159.—SIDE VIEW OF THE BRAIN AND UPPER PART OF THE SPINAL CORD IN PLACE—THE PARTS WHICH COVER THE CEREBRO-SPINAL CENTRES BEING REMOVED.

C. C. the convoluted surface of the right cerebral hemisphere; *Cb.* the cerebellum; *M.Ob.* the medulla oblongata; *B.* the bodies of the cervical vertebræ; *Sp.* their spines; *N.* the spinal cord with the spinal nerves.

upper end passes on into the large *convoluted* structure (*C.C.C.*) which is called the (right) **cerebral hemisphere.**

Lying beneath the hinder end of the hemisphere is a large laminated mass which overhangs the posterior side of the bulb and is known as the **cerebellum** (*Cb.*). When the brain is removed from the skull and looked at from its base or under surface many further details may be at once made out. Thus it becomes evident that the brain consists of two halves, corresponding to each half of the spinal cord, lying symmetrically on each side of a line joining *CC.* and *M.* in Fig. 160. The bulb (*M*) widens out at its upper end and gives off from each side a number of nerves (vii.—xii.) which are analogous to the spinal nerves but, as originating from the brain, are called **cranial nerves.** The other six pairs of cranial nerves (i.—vi.) come off from parts of the brain in front of (above) the bulb. The cerebellum is seen to send out from each side towards the central line a large mass of transverse fibres which sweep across the brain and meet, with a depression in the middle line, thus forming a sort of bridge from one half of the cerebellum to the other; this bridge lies just in front of (above) the bulb and is called the **pons Varolii.** The number VI. is placed upon the *pons* in Fig. 160. The longitudinal nerve fibres of the bulb pass forwards (upwards in the figure), among and between the transverse fibres of the *pons*, and become visible again in front of it as two broad diverging bundles called **crura cerebri,** which plunge into the corresponding **cerebral hemisphere** of each half of the brain.

When the brain is viewed from above nothing is visible beyond the convoluted surfaces of the two cerebral hemispheres, separated by a median fissure whose sides are in close contact. But if the sides of this fissure are carefully pushed apart, the cerebral hemispheres may be seen to be connected with each other by an elongated transverse and horizontal mass of nerve fibres known as the **corpus callosum** (shown as *CC.*, in Fig. 160). If the hinder ends of the cerebral hemispheres are raised, the whole upper surface of the cerebellum comes into view, and if the cerebellum is now lifted up, the *posterior* surface of

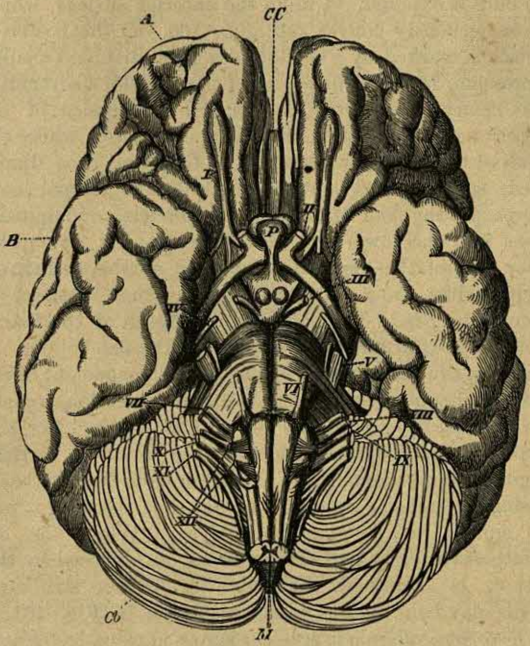


FIG. 160.—THE BASE OR UNDER-SURFACE OF THE BRAIN.

A, frontal lobe; *B*, temporal lobe of the cerebral hemispheres; *Cb.* cerebellum; *I*, the olfactory nerve; *II*, the optic nerve; *III*, *IV*, *VI*, the nerves of the muscles of the eye; *V*, the trigeminal nerve; *VII*, the facial nerve; *VIII*, the auditory nerve; *IX*, the glossopharyngeal; *X*, the pneumogastric; *XI*, the spinal accessory; *XII*, the hypoglossal, or motor nerve of the tongue. The number *VI* is placed upon the *pons Varolii.* The medulla oblongata (*M*) is seen to be really a continuation of the spinal cord; on the lower end are seen the two crescents of grey matter; the section, in fact, has been carried through the spinal cord, a little below the proper medulla oblongata. From the sides of the medulla oblongata are seen coming off the *X*, *XI*, and *XII* nerves; and just where the medulla is covered, so to speak, by the transversely disposed *pons Varolii*, are seen coming off the *VII* nerve, and more towards the middle line the *VI*. Out of the substance of the *pons* springs the *V* nerve. In front of that is seen the well-defined anterior border of the *pons*; and coming forward

the bulb is exposed. Unlike the anterior surface, which is conspicuously convex (see Fig. 160, *M*) the posterior surface is marked by a shallow elongated diamond-shaped depression, forming the cavity of the **fourth ventricle.** This cavity arises from the gradual divergence of the posterior white columns of the spinal cord, while the depth of the posterior fissure is at the same time diminished, so that the central canal of the spinal cord approaches the floor of the fourth ventricle, and actually opens into the lower end of the cavity (Fig. 161); this lower end of the ventricle is known as the **calamus scriptorius,** from its fancied resemblance in shape to the nib of a pen. The narrowed upper end of the fourth ventricle is continued forwards under the cerebellum.

Having thus made out so much of the arrangement of the brain as may be seen by mere external inspection, we may now proceed to examine its internal structure. For this purpose the most instructive method is to cut a vertical, longitudinal section through the brain from front to back, passing through the middle line, and thus dividing it into two similar and symmetrical halves. When the cut surface of the right half of the brain, as exposed by this section, is examined, the following further structural details may be made out, and are shown in Fig. 161.

The *corpus callosum* is seen *cut* across at *cc. cc. cc.* Above this, and extending forwards and backwards, is the flattened *exposed surface* of the right cerebral hemisphere, which forms one side of the median fissure between the hemispheres. The upper end of the spinal cord, *Sp.c.*, passes into the bulb *B*, in front of which the transverse fibres

in front of that line, between the *IV* and *III* nerves on either side, are seen the *crura cerebri.* The two round bodies in the angle between the diverging crura are the so-called *corpora albicantia,* and in front of them is *P*, the pituitary body. This rests on the chiasma, or junction, of the optic nerves; the continuation of each nerve is seen sweeping round the crura cerebri on either side. Immediately in front, between the separated frontal lobes of the cerebral hemispheres, is seen the *corpus callosum, CC.* The fissure of Sylvius, about on a level with *I* on the left and *II* on the right side, marks the division between frontal and temporal lobes.

of the *pons* are seen in section at P, while the longitudinal fibres of the bulb run forward above the pons to emerge in front as one of the (right) *crura cerebri*. Anteriorly this crus disappears out of the section since it diverges to the right (see Fig. 160) from the median line of the brain

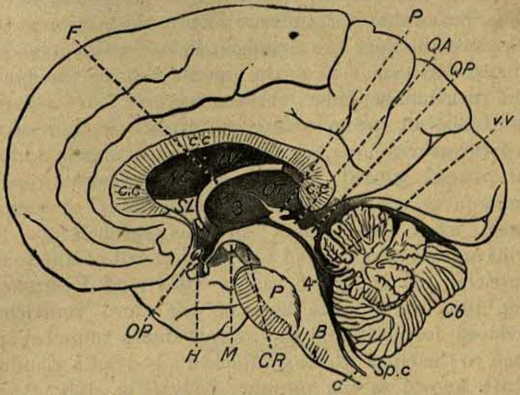


FIG. 161.—VIEW OF THE RIGHT HALF OF A HUMAN BRAIN AS SHOWN BY A LONGITUDINAL SECTION IN THE MEDIAN LINE THROUGH THE LONGITUDINAL FISSURE. (AFTER SHERRINGTON.)

Sp.c. spinal cord; *B*, bulb; *P*, pons; *CR*, *crus cerebri*; *M*, *corpus albicans*; *Cb*, cerebellum; *c*, central canal of spinal cord opening into 4, the fourth ventricle; *V.V*, valve of Vieussens; *QP*, *QA*, *corpora quadrigemina*, beneath which is the *aqueduct of Sylvius* leading from the fourth ventricle into 3, the cavity of the third ventricle; *P*, pineal gland; *F*, fornix or roof of third ventricle; *OT*, *optic thalamus*; *H*, pituitary body; *OP*, optic nerve cut across at the optic decussation (see Figs. 160 and 167); *SL*. a part of the *septum lucidum*, of which the remainder has been cut away to reveal *NC*, *LV*, the cavity of the lateral ventricle; this communicates with the third ventricle by means of the *foramen of Monro*, whose position is marked by a small x at the front end of the third ventricle; *c.c*, *c.c*, *c.c*, *corpus callosum*, above which is the mesial surface of the right cerebral hemisphere.

to enter the corresponding cerebral hemisphere. The cerebellum *Cb*, is seen *in section* overhanging the bulb, and between it and the bulb is the cavity, shaded and marked with a 4, to which we have previously alluded as the *fourth ventricle*. The central canal *c.c.* of the spinal cord is shown

as an opening into the hinder end of the cavity of the fourth ventricle, while the front end of the cavity is prolonged into a narrow passage, the **aqueduct of Sylvius**, which leads into a much larger cavity known as the **third ventricle**, and marked by a 3. Above this aqueduct are *four* largely developed masses of tissue, but of these *two* only are seen in the section at *QA*, *QP*, since the four are arranged in two pairs, one pair being placed each side of the middle line of the brain; from their number (four) these structures have received the name of **corpora quadrigemina.** In front of the corpora quadrigemina is a small structure, seen in section, the **pineal gland**, *P*. The posterior corpus quadrigeminum is continuous with a thin layer of nervous tissue, which leads back into the cerebellum; this forms an overhanging roof to the front end of the fourth ventricle, and is known as the **valve of Vieussens** (Fig. 161, *v.v.*). The floor of the third ventricle is produced forwards and downwards into a funnel-shaped space, to the tip of which is attached a body of a glandular nature known as the pituitary body (Fig. 160, *P*, and Fig. 161, *H*). The roof of the third ventricle is provided by a layer of tissue seen *in section* and known as the **fornix** (Fig. 161, *F*); this is connected posteriorly with the hinder end of the *corpus callosum*, and in front it curves downwards and backwards into the lateral wall of the third ventricle towards the **corpus albicans**, *M*. The *vertical* space between the fornix and the corpus callosum is filled in by a thin *double* layer of nervous tissue; this is known as the **septum lucidum.** It lies in the plane of the paper on which the figure is printed, but only a small portion of it is shown at *SL*. The remaining part has been cut away in order to reveal a feature of which, so far, no mention has been made, viz., the darkly shaded cavity *NC.*, *LV.*, lying in the middle of the cerebral hemisphere, and known as the (right) **lateral ventricle.** The cavity of this ventricle communicates with that of the third ventricle by a small opening at *x*, the **foramen of Monro.** Since

the septum lucidum consists of two layers there is a small flattened closed space between these layers in the middle line of the brain ; this is spoken of as the **fifth ventricle**, but it has no actual connection with the other ventricles.[1] (See Fig. 163, 5.) Each lateral ventricle is a cavity of a very peculiar shape, one branch running forwards towards the front end of the hemisphere and one backwards towards the hinder end, and from the latter a third branch runs downwards and once more forwards. These correspond respectively to the chief **lobes** of which each hemisphere is made up, namely the **frontal** lobe, the **parietal** and

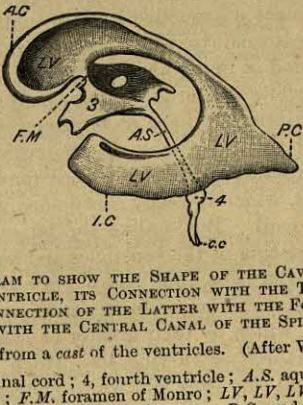


FIG. 162.—DIAGRAM TO SHOW THE SHAPE OF THE CAVITY OF THE LEFT LATERAL VENTRICLE, ITS CONNECTION WITH THE THIRD VENTRICLE, AND THE CONNECTION OF THE LATTER WITH THE FOURTH VENTRICLE, AND HENCE WITH THE CENTRAL CANAL OF THE SPINAL CORD.

Drawn from a *cast* of the ventricles. (After Welcker.)

c.c. canal of spinal cord ; 4, fourth ventricle ; *A.S.* aqueduct of Sylvius ; 3, third ventricle ; *F.M.* foramen of Monro ; *LV*, *LV*, *LV*, lateral ventricle with its anterior cornu, *A.C.*, posterior cornu, *P.C.*, and inferior cornu, *I.C.*

occipital lobes, and the **temporal** lobe. These lobes are marked off on the surface of the hemispheres by **fissures**, of which the most conspicuous are the **fissure of Sylvius**, and the **fissure of Rolando**. (See Fig. 168).

The cerebellum is firmly connected to the rest of the brain by the transverse fibres which help to form the

[1] The two lateral ventricles, one in each cerebral hemisphere, are reckoned as the first and second ventricles ; hence the space between the layers of the septum lucidum is known as the fifth ventricle.

pons Varolii (Fig. 160), and constitute the **middle peduncle** of each half of the cerebellum. But each half has a further attachment by means of two other bands of fibres. Of these one coming out of the central (medullary) part of the cerebellum on each side, runs forwards towards, and disappears under, the corpora quadrigemina; this forms the **superior peduncle.** The other runs backwards towards the bulb and merges, as the **inferior peduncle,** into that part of the bulb which is a continuation upwards of the lateral columns of white matter of the spinal cord.

We have seen that the spinal cord consists essentially of a central canal surrounded by grey matter containing nerve cells, external to which is a covering of white matter composed of nerve fibres; and the arrangement of the grey and white matter is comparatively simple. Now from the description we have so far given of the brain, it is evident that the brain may also be regarded as being built up of structures which are placed round the sides of a central canal, which is really continuous with the canal of the spinal cord. But, unlike the latter, the canal of the brain, consisting of the ventricles and aqueduct, is not a simple straight tube, but has a very peculiar shape. Moreover, although the brain is made up of grey and white matters, which by their greater or less development form the structures of varying size which make up the brain as a whole, the grey and white matters are not arranged in any simple way as they are in the spinal cord. On the contrary, although in the brain a great deal of the grey matter is placed externally to the white, the latter is interspersed with localised deposits of grey matter, some large, some small, which give to the whole an extraordinary complexity. And this complexity is still further increased by the existence of strands or bundles of nerve fibres, which serve to interconnect all these various deposits of grey matter, so as to ensure the possibility of co-ordinated action between the

individual parts of which the brain as a whole is built up. It would be neither possible nor desirable to attempt to deal in any detail in this book with the varied arrangements of the several deposits of grey matter in the brain, and with their connections by strands of white matter. But some of them stand out so conspicuously as structures, and are so important in their functions, that we must of necessity take them into consideration.

The Corpora Quadrigemina.—These have already been described as four conspicuous masses of tissue lying in two pairs above the aqueduct of Sylvius. They consist of deposits of grey matter in the otherwise thin wall of the roof of the aqueduct. Each deposit is surrounded by white matter, and from each bands of fibres run obliquely downwards and forwards, those from the anterior pair of the corpora making connection with structures connected with the optic nerve (Fig. 160, *II.*), while those from the posterior pair are believed to make similar connections with the nerves concerned in hearing (Fig. 160, *VIII.*).

The Optic Thalami.—The longitudinal fibres of the bulb, passing between the transverse fibres of the pons reappear, as we have seen, in front of the pons as the *crura cerebri.* These diverge from the middle line to enter the cerebral hemispheres. As each crus passes into the base of the corresponding hemisphere, it receives on its *upper* surface a large deposit of grey matter placed somewhat obliquely across its course; this mass of grey matter is the **optic thalamus.** Lying thus to one side of the third ventricle, and under the lateral ventricle, it is easily seen how each optic thalamus comes to form a projection in the outer side-wall of the third ventricle, and on the floor of the lateral ventricle. Thus the optic thalamus is shown at *O.T.* in Fig. 161, as part of the wall of the third ventricle, and as *O.T.* in Fig. 163, which represents in diagram a *horizontal* section through the hemispheres passing above the floor of the lateral

ventricles. The inner sides of the optic thalami are connected by a small commissure (Fig. 163, *C.*), which extends across the third ventricle; their outer sides are imbedded in the substance of the cerebral hemispheres with which they are connected by nerve fibres, and from

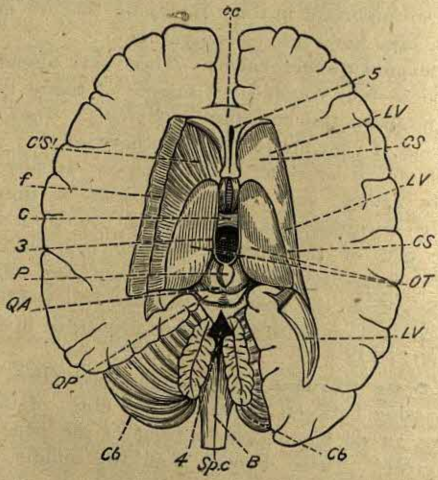


FIG. 163.—DIAGRAM OF A HORIZONTAL SECTION OF THE BRAIN ABOVE THE FLOOR OF THE LATERAL VENTRICLES. (AFTER HIRSCHFELD AND LEVEILLÉ.)

Sp.c. spinal cord; *B*, bulb; *Cb*, *Cb*, cerebellum; 4, fourth ventricle; *Q.P.*, *Q.A*, corpora quadrigemina; *P*, pineal gland; 3, third ventricle; 5, fifth ventricle; *cc*, front part of corpus callosum; *LV*, *LV*, *LV*, lateral ventricle; *OT.*, optic thalami; *CS*, *CS*, corpus striatum; *C*, commissure of optic thalami. On the left side *CS'* marks the corpus striatum, into which an incision has been made and a flap, *f.*, turned back to show its internal striated appearance.

their hinder end a bundle of fibres sweeps forward to pass into the tract of the optic nerves.

The Corpora Striata.—Each corpus striatum may be regarded as a mass of grey matter deposited obliquely, as was each optic thalamus, on the course of the crura

cerebri, but lying somewhat in front of the optic thalami. Hence the corpora striata are seen as a projection on the floor of the lateral ventricles (Fig. 163, *C.S.*, *C.S.*), and as part of the side wall of the front end of this ventricle (Fig. 161, *NC.*). Each corpus consists of two parts, one lying in front of the optic thalamus, the other further back and by the side of the thalamus. The larger part of each corpus striatum is imbedded in the neighbouring substance of the cerebral hemisphere, with which it is intimately connected by nerve fibres. It is also similarly connected with the fibres of the crus on which it lies.

A clear understanding of the position and relations of the optic thalami and corpora striata is essential in connection with the course of a tract of nerve fibres with which we shall deal later, known as the **internal capsule.**

The Membranes of the Brain.—The brain is invested by three membranes which are the same in name, and similarly placed and related to each other as those which we have previously described as covering the spinal cord (see p. 453). Of these the pia mater is highly vascular, and carries blood-vessels down into the grey matter, especially in the **sulci** or grooves to which the convoluted appearance of the surface of the brain is due. Moreover, it forms a roof to the hinder part of the cavity of the fourth ventricle, and a highly developed layer of the pia mater is tucked in under the hinder end of the cerebral hemispheres to form the roof of the third ventricle; this is known as the **velum interpositum.** The edges of this velum as it lies beneath the *fornix* project on each side into the cavities of the lateral ventricles and are here known as the **choroid plexuses**, the whole being arranged with a view to the nutrition of the internal parts of the brain. The cavities of the cerebral ventricles, and hence of the central canal of the spinal cord, are placed in communication with the *subarachnoid space*, by

a small opening in the pia mater covering the hinder end of the fourth ventricle; this opening is known as the **foramen of Magendie.**

11. The Minute Structure of the Brain.—In the spinal bulb the arrangement of the white and grey matter is substantially similar to that which obtains in the spinal cord, that is to say, the white matter is external and the grey internal; but the grey matter, containing, as in the spinal cord, nerve cells, is more abundant than in the spinal cord, and the arrangements of white and grey matter become much more intricate and complex. The structure of the white matter of the brain is essentially the same as that of the spinal cord.

Above the bulb there are internal deposits of grey matter, containing nerve cells, at various places, more especially in the pons Varolii, the crura cerebri, the corpora quadrigemina, optic thalami and corpora striata. And there is a remarkably shaped deposit of grey matter in the interior of the cerebellum, on each side. But what especially characterises the brain is the presence of grey matter of a special nature, containing peculiarly shaped nerve cells, on the surface of the cerebral hemispheres known as the **cortex**, and similarly a special grey matter forms the surface of the cerebellum. This superficial grey matter covers the whole surface of both these organs, dipping down into the fissures (sulci) of the former, and following the peculiar plaits or folds into which the latter is thrown.

The Cerebellum.—The surface of the cerebellum presents a corrugated or laminated appearance. When a section is made through one of its hemispheres it is seen that the depressions which separate the laminæ give off secondary lateral depressions as they pass towards its centre, so that the surface is really divided up into a very large number of leaf-like foldings which are known as the **lamellæ**. The central part of the cerebellum consists of white matter which is essentially the same as the white

matter of the spinal cord, that is to say, it is made up chiefly of medullated nerve fibres. Portions of this white matter extend outwards into the primary foldings and secondary lamellæ of the cerebellar surface, and are covered by grey matter, the arrangement thus presenting a very characteristic arborescent appearance when seen in section.[1]

When a section of the external grey matter is cut at right angles to the surface of a lamella, stained, and examined under the microscope, it is found to consist of two layers. The innermost, lying next to the central white matter, is made up of a large number of small closely-packed cells supported by neuroglia (see p. 465) and is known as the **nuclear layer** (Fig. 164, *N*). The outer layer, immediately under the pia mater, shows a few cells, but the chief appearance it presents is that of a granular mass made up of closely-set dots. These dots are in reality the cut ends of fibres of which some belong to the supporting neuroglia, but of which the majority are nerve fibrils. From its punctated appearance (Fig. 164, *x*.) this layer, which is much broader than the nuclear layer, is known as the **molecular layer** (Fig. 164, *M*.). Between these two layers lies a row of nerve cells of very striking and characteristic appearance, known as the **cells of Purkinjé** (Fig. 164, 1). These are pear-shaped, with a large and conspicuous nucleus, the bulbous inner end resting on the nuclear layer, while the outer end divides into a large number of processes which run out into the molecular layer as finer and finer branches. The granular appearance of the molecular layer is in part due to the close juxtaposition of the cut ends of these branches or *dendrites* from the cells of Purkinjé. The inner end of each cell bears a single process which is usually cut through near the cell but is really prolonged down into the central white matter as a medullated nerve fibre. Such are the details which can be made out

1 This is somewhat imperfectly shown in Figs. 161 and 163.

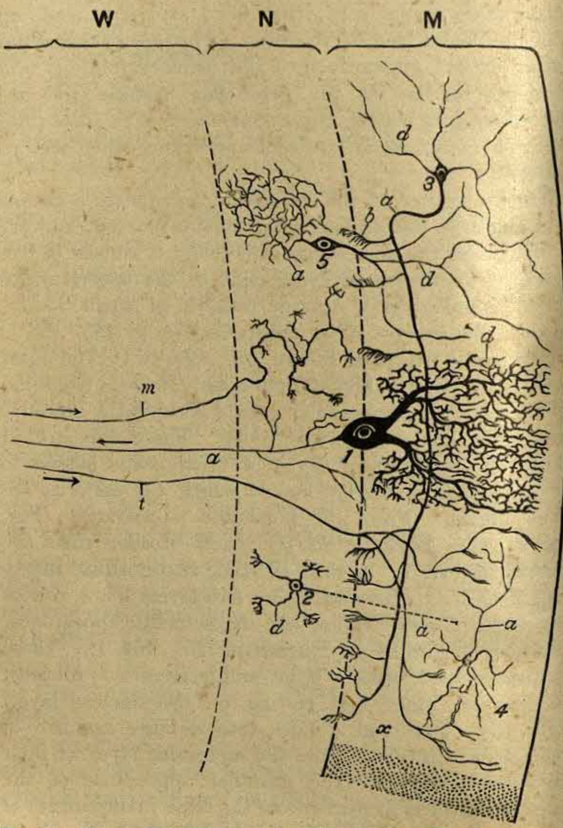


FIG. 164.—DIAGRAM TO ILLUSTRATE THE STRUCTURE OF THE SUPERFICIAL GREY MATTER OF THE CEREBELLUM AS SEEN IN A TRANSVERSE SECTION OF A LAMELLA.

M, molecular layer; *N*, nuclear layer; *W*, central white matter; 1, cell of Purkinjé; 2, spider-cell; 5, cell of Golgi; 3, basket-cell with one of its baskets, *b*; 4, another kind of cell in the molecular layer; *t*, tendril fibre; *m*, moss-fibre.

In the case of each cell *a* is the axon or main undivided process, *d* is a dendrite or divided process.

in an ordinarily stained section. But by employing special methods of staining many further details come into view, and putting all these together we are justified in constructing the preceding diagrammatic Figure 164 to show the nature and relationships of the cells of the cerebellar cortex and of its two layers to the fibres of the central white matter.

In this figure the cells which call for special attention are the following. The cell of Purkinjé (1) with its central axon (*a*) and peripheral dendrites (*d*). The basket-cell (3) with its axon (*a*) and baskets (*b*); the baskets in reality surround the bodies of cells of Purkinjé which, for the sake of clearness are not shown in the diagram. The spider-cell (2) in the nuclear layer with its axon (*a*) running into the molecular layer and dendrites (*d*). Also in addition to the fibre derived from the inner end of the cell of Purkinjé it is important to notice the moss-fibre (*m*) whose outer end terminates by branching in the nuclear layer and the tendril-fibre (*t*) which passes further outwards but ends similarly in the molecular layer. The direction in which impulses are supposed to travel along these fibres is indicated by arrows.

The Cerebral Cortex.—The structure of the superficial grey matter of the cerebellum is practically the same in each part of the cerebellar cortex. In the cerebrum, on the other hand, the details of structure vary not inconsiderably according to the region of the cortex from which a section is prepared. Into these differences we cannot enter, but must content ourselves with a somewhat diagrammatic description and figure in illustration of the general structural arrangement of the cells and fibres of the cortex as a whole.

The grey matter is permeated throughout its whole thickness by a neuroglia which is essentially the same as that of the rest of the central nervous system. This forms the supporting tissue in which the nerve cells of the cortex are imbedded and through

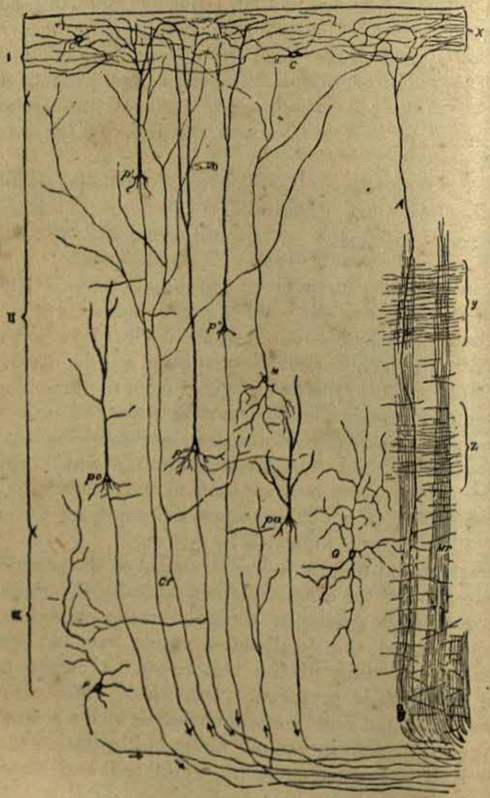


FIG. 165.—DIAGRAMMATIC FIGURE TO ILLUSTRATE THE STRUCTURE OF A TYPICAL SECTION OF THE CEREBRAL CORTEX.

I. Molecular layer. *II.* Layer of pyramidal cells. *III.* Layer of polymorphous cells.

c and *c′*, cells of the molecular layer; *p′*, *p″*, *p‴*, pyramidal cells; *P*, cell of the polymorphous layer; *m.r.* medullary ray of nerve fibrils from central white matter; *x*, *y*, *z*, tangential bundles of nerve fibrils.

which the fibrils of nerves pass to and from these cells from the central white matter. The latter is composed, as in the cerebellum, of medullated nerve fibres. This neuroglia is most marked in the outermost parts of the cortex, immediately below the pia mater, and since in a section its wavy fibres are mostly seen as sectional dots, this layer of the cortex is known as the **molecular layer** (Fig. 165, *I*). Internally to this layer the cortex is characterised by the presence of nerve cells whose shape is pyramidal with the apex of each cell pointed towards the surface of the brain. This layer may therefore be spoken of as the **layer of pyramidal cells** (Fig. 165, *II*). These cells vary in size in the several parts of this layer, the largest being found in the inner portion, the smallest next to the molecular layer. That part of the cortex which lies immediately external to the central white matter is characterised by the presence of nerve cells of a somewhat irregular form, hence this layer is known as the **layer of polymorphous cells** (Fig. 165, *III*).

In addition to the nerve cells and their processes which characterise the several layers of the cortex, nerve fibrils pass up into and through the cortex from the central white matter. Of these some are arranged in bundles at right angles to the surface of the cortex, **medullary rays** (Fig. 165, *m.r.*) while others lie parallel to the surface as **tangential rays** (Fig. 165, *x.y.z.*).

12. The Cranial Nerves.—Nerves are given off from the brain in pairs, which succeed one another from before backwards, to the number of twelve (Figs. 160 and 166). These are often called "*cranial*" nerves, to distinguish them from the spinal nerves.

The *first pair*, counting from before backwards, are the **olfactory nerves**, and the *second* are the **optic nerves**. The functions of these have already been described. But these two nerves require special notice. That which is commonly called the olfactory "nerve" is really a lobe

of the brain and contains nerve cells. The proper olfactory nerves are bundles of fibres which proceed from the under surface of the above and traverse the cribriform plate to be distributed to the olfactory mucous membrane. And it is an extremely remarkable fact that these fibres closely resemble the non-medullated fibres of the sympathetic nerves, in being hardly anything more than neuraxes, bearing nuclei at intervals. A sheath, apparently representing the neurilemma, is however present in each fibre.

The optic "nerve" is also properly speaking a lobe of the brain, and it retains its character as a part of the central nervous system in so far as its fibres have no neurilemma and are nodeless, but it contains no nerve cells along its course.

The *third pair* is called **motor oculi** (mover of the eye), because they are distributed to all the muscles of the eye except two.

The nerves of the *fourth pair*, **trochlear**, and of the *sixth pair*, **abducens**, supply, each, one of the muscles of the eye, on each side; the fourth going to the **superior oblique muscle**, and the sixth to the **external rectus.** Thus the muscles of the eye, small and close together as they are, receive their nervous stimulus by three distinct nerves.

Each nerve of the *fifth pair* is very large. It has two roots, a motor and a sensory, and further resembles a spinal nerve in having a ganglion on its sensory root. It is the nerve which supplies the skin of the face and the muscles of the jaws, and, having three chief divisions, is often called **trigeminal.** One branch containing sensory fibres supplies the fore-part of the mucous membrane of the tongue, and is often spoken of as the *gustatory*.

The *seventh pair* furnish with motor nerves the muscles of the face, and some other muscles, and are called **facial.**

The *eighth pair* are the **auditory** nerves. The auditory is, as we have seen (p. 392), divided into the cochlear and vestibular nerve. (See later, p. 523).

The *ninth pair*, or **glossopharyngeal** nerves, are mixed nerves; each being, partly, a nerve of taste, and supplying the hind-part of the mucous membrane of the tongue, and, partly, a motor nerve for the pharyngeal muscles.

The *tenth pair* is the two **pneumogastric** nerves, often called the **vagus**. These very important nerves, and the next pair, are the only cranial nerves which are distributed to regions of the body remote from the head. The pneumogastric supplies the larynx, the lungs, the liver, and the stomach, and branches of it are connected with the heart.

The *eleventh pair* again, called **spinal accessory**, differ widely from all the rest, in arising, in part, from the sides of the spinal cord, between the anterior and posterior roots of the cervical nerves. They run up, gathering fibres as they go, to the medulla oblongata, and then leave the skull by the same aperture as the pneumogastric and glossopharyngeal. They are purely motor nerves, supplying certain muscles of the neck, while the pneumogastric is mainly sensory, or at least afferent.

The *twelfth pair*, or **hypoglossal** nerves, are the motor nerves which supply the muscles of the tongue.

Of these nerves, the two foremost pairs do not properly deserve that name, but are, as we have said, really processes of the brain. The olfactory pair are prolongations of the cerebral hemispheres; the optic pair, of the walls of the third ventricle.

The optic nerve from each eye meets its fellow nerve from the other eye at the base of the brain below the third ventricle. Here they cross each other in what is called the **optic chiasma** (covered by the pituitary body *P* in Fig 160) and are continued on backwards,

to make connection with the brain, as the **optic tracts.**

These are connected, as already stated, with the hinder part of the optic thalami and with the anterior pair of corpora quadrigemina. At the chiasma the fibres of the optic nerves undergo a remarkable partial decussation. The fibres from each half of the retina *nearest to the nose cross*

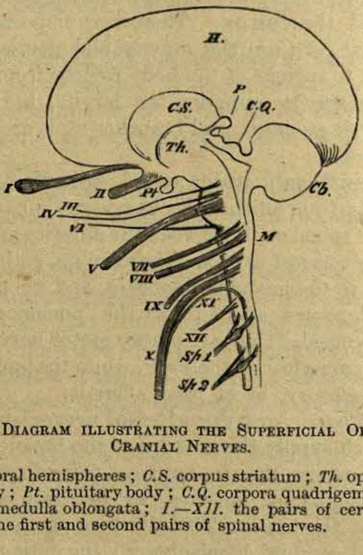


Fig. 166.—A Diagram illustrating the Superficial Origin of the Cranial Nerves.

H, the cerebral hemispheres; *C.S.* corpus striatum; *Th.* optic thalamus; *P.* pineal body; *Pt.* pituitary body; *C.Q.* corpora quadrigemina; *Cb.* cerebellum; *M.* medulla oblongata; *I.—XII.* the pairs of cerebral nerves; *Sp.* 1, *Sp.* 2, the first and second pairs of spinal nerves.

over to the opposite side of the brain; the fibres from the other half of each retina pass into the brain without crossing. Hence the right optic tract contains the fibres from the nasal half of the left retina and from the other or temporal half of the right retina, and similarly the left optic tract is made up of the fibres of the temporal

half of the left retina and the nasal half of the right retina. This arrangement is essential to the eye as a sense-organ with reference to what we have previously spoken of as "corresponding points and single vision with two eyes" (see p. 445). Going through the optic chiasma, there are also fibres joining one side of the brain to the other *via* the optic tracts and probably fibres joining the two eyes.

13. The Functions of the Spinal Bulb or Medulla Oblongata.—The bulb plays so important a part in the economy of the body that we may almost enumerate its functions by recalling all the instances in which we have

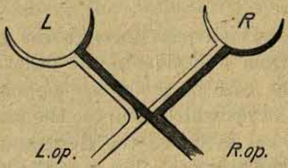


FIG. 167.—DIAGRAM TO ILLUSTRATE THE DECUSSATION OF FIBRES IN THE OPTIC CHIASMA.

R, right eye; *L*, left eye; *R.Op.* right optic tract; *L.Op.* left optic tract. The decussation is shown by the distribution of the right (shaded) and the left (unshaded) tract to the retinas of the two eyes.

made mention of its activities in the earlier lessons of this book. Thus we have seen that it contains a centre which gives rise to the contractions of the respiratory muscles and keeps the respiratory pump at work, so that injuries to the bulb may arrest the respiratory process (p. 158). Further it contains centres for the regulation of the heart-beat (p. 77) and of the condition of the blood-vessels over the whole body (p. 69). But beyond these the bulb also contains centres for the nervous act of swallowing, for the reflex secretion of saliva, and for many other actions. Thus we find that simple puncture of one side

of the floor of the fourth ventricle produces for a while an increase of the quantity of sugar in the blood, beyond that which can be utilised by the organism. The sugar passes off by the kidneys, and thus this slight injury to the medulla produces a temporary disorder closely resembling the disease called *diabetes*. Hence we speak of a diabetic centre in the bulb. Beyond this the bulb acts as a great conductor of impulses; for all impulses passing up and down between the higher parts of the brain and the spinal cord must make their way through the bulb from or to the spinal nerves. And a similar statement holds good for impulses along the cranial nerves, with the exception of the olfactory, optic and third and fourth nerves.

The impulses which pass through the bulb cross, for the most part, from one side to the other on their way along it. In the case of the *crossed pyramidal tract* the crossing of the fibres which compose the tract takes place by means of what is called the **decussation of the pyramids** in the anterior columns of the bulb (Fig. 172). This point is indicated in Fig. 160 by a group of small converging marks on the surface of the bulb just above the cut end marked *M*. The fibres of the small *direct pyramidal tract* cross below the bulb in the spinal cord by means of its anterior white commissure (see Fig. 143). Similarly the fibres concerned in the transmission of afferent impulses largely cross in the bulb by paths which are varied but of which one is well marked as the **sensory decussation**. This general decussation of efferent and afferent fibres leads to the result that disease or injury of one side of the brain affects the opposite side of the body. Thus when, as not unfrequently happens, a blood-vessel gives way in the right cerebral hemisphere, leading to a destruction of nervous matter there, the result is that the left arm, and left leg, and left side of the body generally are paralysed, that is, the will has no longer any power to move the muscles of

that side, and impulses started in the skin of that side cannot awaken sensations in the brain.

But there is also a decussation of impulses in the case of the nerves arising from the medulla above the decussation of the pyramids. Thus, in the case quoted above of a blood vessel bursting in the right cerebral hemisphere, the left side of the man's face is paralysed as well as the left side of his body, that is to say, impulses cannot pass to and from his brain and the left facial and fifth nerves. The impulses along these nerves also decussate, and reach the right side of the brain.

It sometimes happens, however, that disease or injury may affect the medulla oblongata itself, on one side only (*e.g.* the right), above the decussation of the pyramids, in such a way that the fifth and facial nerves are affected in their course before they decussate, that is to say, on the same side as the injury. The man then, while still paralysed on the left side of his body, is paralysed on the right side of his face.

14. The Functions of the Cerebellum.—When speaking of reflex actions we pointed out (p. 487) that the complicated movements of walking when once started by the will are essentially reflex in their continued production. Moreover we also drew attention to the fact that the *co-ordination* of the efferent impulses which, although distributed to many different muscles, give rise by their united action to the *orderly* movements of walking, is dependent upon afferent impulses from various parts of the body. Thus walking becomes unsteady or even impossible in the absence of the normal sensory impulses from the skin, or of visual impulses from the eyes; and to these we might have added afferent impulses from the sensory nerves of the muscles themselves. When we take cases of movements which are less obviously reflex, that is more strictly voluntary, than are those of walking, we find that here again their orderly or co-ordinated production depends largely on tactile and visual impulses.

Now experiment and observation in cases of disease have shown quite conclusively that *the one great function of the cerebellum is to play a most important part in the co-ordination of the actions, nervous and muscular, by which the movements of the body are carried on.*

After the cerebellum has been completely removed, an animal does not differ in any essential respect from its normal condition as regards its intelligence or its special senses, such as sight or hearing. But with regard to its movements a great difference is observed in the absence of the cerebellum; all movements are now clumsily executed—there is a want of orderliness or co-ordination. This statement sums up our knowledge of the function of the cerebellum.

We do not know *how* the cerebellum works in thus keeping an orderly grip over the mechanisms of movement; but we see how easily it may do so when we consider its connections with the spinal cord and with the rest of the brain. We saw (p. 494) that the cerebellum as well as the cerebrum sends fibres which connect with the motor neurons in the anterior horn and (p. 491) that two large tracts of afferent fibres from the spinal cord pass into the cerebellum, viz. the *cerebellar tract* by the inferior peduncle and the ascending *antero-lateral tract* by the superior peduncle. Moreover the cerebellum is connected with that part of the bulb in which the *posterior column* ends. Thus it may be a recipient of a vast number of afferent sensory impulses, which are so essential for co-ordinated movement. But each half of the cerebellum is further connected with the cortex of the cerebral hemisphere of the *opposite side* in two ways, firstly, by the fibres of its middle peduncle across the pons Varolii, and secondly, and more directly, by fibres in its superior peduncle (see p. 506). And we shall see that it is exactly in the cortex of the cerebral hemispheres that impulses chiefly arise for the initiation of muscular movements.

When describing the arrangements of the internal ear, it was stated that the semicircular canals have functions other than that of hearing. Now the auditory nerve consists of two quite distinct parts, the *cochlear nerve*, which is distributed to the cochlea, and the *vestibular nerve*, which is distributed to the vestibule, the utricle, saccule, and semicircular canals. These two nerves, the axons of which originate in the ear, terminate in connection with groups of cells lying in the spinal bulb, and the group of cells associated with the vestibular nerve is directly connected by a strand of fibres with the cerebellum. Thus there is a path by which afferent (sensory) impulses from the semicircular canals may directly reach the cerebellum and there be turned to account in the co-ordination of movements. Bearing this in mind, it is not surprising to find that the semicircular canals play a very important part in the guidance of co-ordinated movement.

The semicircular canals lie in three planes at right angles to each other (p. 392). When any *one* of the canals is experimentally injured, the animal executes a series of oscillatory movements of the head, which are, broadly speaking, in the plane of that canal. When all three canals are injured, the animal is thrown into continuous movements of the most varied and often extraordinary kind, and has lost all power of *balancing* itself in a normal way. Not infrequently in man these canals undergo injury as the result of disease, and in this case the feelings experienced by the patient are those of extreme giddiness, and an inability to balance the body, while the symptoms exhibited to an onlooker are those of a want of co-ordination in the execution of movements. Thus there is no doubt that the semicircular canals are of very great importance as organs such that *impulses arising in them enable us to maintain our bodily equilibrium*, and there are reasons for thinking that the utricle and saccule also have a very similar function.

15. The Functions of the Cerebral Hemispheres.— The Hemispheres the Seat of Intelligence and Will.— The functions of most of the parts of the brain which lie in front of the spinal bulb are, at present, very ill understood; but it is certain that extensive injury, or removal, of the cerebral hemispheres puts an end to intelligence and voluntary movement, and leaves the animal in the condition of a machine, working by the reflex action of the remainder of the cerebro-spinal axis.

We have seen that in the frog the movements of the body which the spinal cord alone, in the absence of the whole of the brain, including the bulb, is capable of executing, are of themselves strikingly complex and varied. But none of these movements arise from changes originating within the organism, they are not what are called voluntary or spontaneous movements; they never occur unless the animal be stimulated from without. Removal of the cerebral hemispheres is alone sufficient to deprive the frog of all spontaneous or voluntary movements; but the presence of the bulb and other parts of the brain (such as the corpora quadrigemina, or what corresponds to them in the frog, and the cerebellum) renders the animal master of movements of a far higher nature than when the spinal cord only is left. In the latter case the animal does not breathe when left to itself, lies flat on the table with its fore-limbs beneath it in an unnatural position; when irritated kicks out its legs, and may be thrown into actual convulsions, but never jumps from place to place; when thrown into a basin of water falls to the bottom like a lump of lead, and when placed on its back will remain so, without making any effort to turn over. In the former case the animal sits on the table, resting on its front limbs, in the position natural to a frog; breathes quite naturally; when pricked behind jumps away, often getting over a considerable distance; when thrown into water begins at once to swim, and continues swimming until it finds some object on which it

can rest; and when placed on its back immediately turns over and resumes its natural position. Not only so, but the following very striking experiment may be performed with it. Placed on a small board it remains perfectly motionless so long as the board is horizontal; if, however, the board be gradually tilted up so as to raise the animal's head, directly the board becomes inclined at such an angle as to throw the frog's centre of gravity too much backwards, the creature begins slowly to creep up the board, and, if the board continues to be inclined, will at last reach the edge, upon which when the board becomes vertical he will seat himself with apparent great content. Nevertheless, though his movements when they do occur are extremely well combined and apparently identical with those of a frog possessing the whole of his brain, he never moves spontaneously, and never stirs unless irritated.

Thus the parts of the brain below the cerebral hemispheres constitute a complex nervous machinery for carrying out intricate and orderly movements, in which afferent impulses play an important part, though they do not give rise to clear or permanent affections of consciousness.

There can be no doubt that the cerebral hemispheres are the seat of powers, essential to the production of those phenomena which we term intelligence and will; and there is experimental and other evidence which seems to indicate a connection between particular parts of the surface of the cerebral hemispheres, and particular acts. Thus irritation of particular spots in the anterior part of a dog's brain will give rise to particular movements of this or that limb, or of this or that group of muscles; and the destruction of a certain part of the posterior lobes of the cerebral hemispheres is said to cause blindness. But the exact way in which these effects are brought about is not yet thoroughly understood; and even if it should be ultimately proved beyond all doubt, that the central end-

organ of vision (p. 421) consists of certain nerve-cells lying in a particular part of the posterior surface of the cerebral hemisphere, and that the central end-organ of hearing (p. 386) consists of other nerve-cells lying elsewhere on the cerebral surface, it will still leave us completely in the dark as to what goes on in the cerebral hemispheres when we think and when we will.

There is no doubt that a molecular change in some part of the cerebral substance is an indispensable antecedent to every phenomenon of consciousness. And it is possible that the progress of investigation may enable us to map out the brain according to the psychical relations of its different parts. But supposing we get so far as to be able to prove that the irritation of a particular fragment of cerebral substance gives rise to a particular state of consciousness, the reason of the connection between the molecular disturbance and the psychical phenomenon appears to be out of the reach, not only of our means of investigation, but even of our powers of conception.

Reflex Actions of the Brain. — Even while the cerebral hemispheres are entire, and in full possession of their powers, the brain gives rise to actions which are as completely reflex as those of the spinal cord.

When the eyelids wink at a flash of light, or a threatened blow, a reflex action takes place, in which the afferent nerves are the optic, the efferent the facial. When a bad smell causes a grimace, there is a reflex action through the same motor nerve, while the olfactory nerves constitute the afferent channels. In these cases, therefore, reflex action must be effected through the brain, all the nerves involved being cerebral.

When the whole body starts at a loud noise, the afferent auditory nerve gives rise to an impulse which passes to the medulla oblongata, and thence affects the great majority of the motor nerves of the body.

It may be said that these are mere mechanical actions, and have nothing to do with the operations which we

associate with intelligence. But let us consider what takes place in such an act as reading aloud. In this case, the whole attention of the mind is, or ought to be, bent upon the subject matter of the book; while a multitude of most delicate muscular actions are going on, of which the reader is not in the slightest degree aware. Thus the book is held in the hand, at the right distance from the eyes; the eyes are moved from side to side, over the lines and up and down the pages. Further, the most delicately adjusted and rapid movements of the muscles of the lips, tongue, and throat, of the laryngeal and respiratory muscles, are involved in the production of speech. Perhaps the reader is standing up and accompanying the lecture with appropriate gestures. And yet every one of these muscular acts may be performed with utter unconsciousness, on his part, of anything but the sense of the words in the book. In other words they are reflex acts.

Similar remarks apply to the act of "playing at sight" a difficult piece of music. The reflex actions proper to the spinal cord itself are *natural*, and are involved in the structure of the cord and the properties of its constituents. By the help of the brain we may acquire an infinity of *artificial* reflex actions, that is to say, an action may require all our attention and all our volition for its first, or second, or third performance, but by frequent repetition it becomes, in a manner, part of our organisation, and is performed without volition, or even consciousness.

As every one knows, it takes a soldier a long time to learn his drill—for instance, to put himself into the attitude of "attention" at the instant the word of command is heard. But, after a time, the sound of the word gives rise to the act, whether the soldier be thinking of it, or not. There is a story, which is credible enough, though it may not be true, of a practical joker, who, seeing a discharged veteran carrying home his dinner, suddenly called out "Attention!" whereupon the man instantly brought his hands down, and lost his mutton and potatoes in the gutter.

The drill had been thorough, and its effects had become embodied in the man's nervous structure.

The possibility of all education (of which military drill is only one particular form) is based upon the existence of this power which the nervous system possesses, of organising conscious actions into more or less unconscious, or reflex, operations. It may be laid down as a rule, which is called the Law of Association, that if any two mental states be called up together, or in succession, with due frequency and vividness, the subsequent production of the one of them will suffice to call up the other, and that whether we desire it or not.

The object of intellectual education is to create such indissoluble associations of our ideas of things, in the order and relation in which they occur in nature ; that of a moral education is to unite as fixedly the ideas of evil deeds with those of pain and degradation, and of good actions with those of pleasure and nobleness.

Localisation of Function in the Cortex of the Cerebral Hemispheres.—We have already alluded (p. 525) to the fact that there is a connection between particular parts of the surface of the cerebral hemispheres and particular acts or special sensations. The possibility thus indicated is of extraordinary importance and must now be dealt with in some detail.

The cerebral hemispheres are separated along the middle line of the brain by a narrow deep fissure across which the corpus callosum passes as a bridge from one hemisphere to the other (see Figs. 160 and 161). The surface of each hemisphere is folded into a large number of **convolutions** or **gyri** separated from each other by sinuous depressions or **sulci** (see Fig. 159, *C.C.*). Some of these depressions are deeper and more marked than others, and are spoken of as **fissures**. Of these the most conspicuous are known as the **fissure of Sylvius**, the **fissure of Rolando**, the **parieto-occipital fissure**, and the **calcarine fissure**. The

position of these is shown in the accompanying diagrams. These fissures may be taken as roughly dividing the surface of the brain more or less distinctly into several

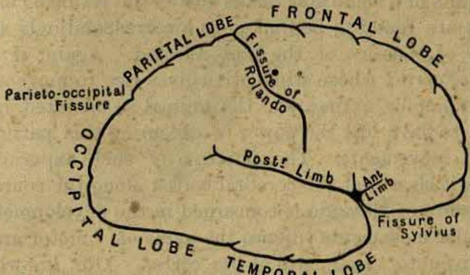


FIG. 168.—DIAGRAM OF OUTER SURFACE OF THE RIGHT CEREBRAL HEMISPHERE.

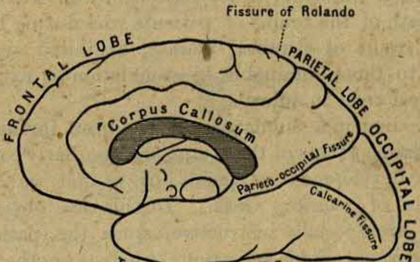


FIG. 169.—DIAGRAM OF THE INNER (MESIAL) SURFACE OF THE RIGHT HEMISPHERE TO SHOW THE PARIETO-OCCIPITAL AND CALCARINE FISSURES.

The *corpus callosum* is seen shaded in section.

lobes, frontal, parietal, occipital, and temporal. The extent of these is shown on Figs. 168 and 169.

When the surface of the hemisphere is stimulated

electrically close to the fissure of Rolando along its anterior margin, very definite movements take place in the limbs of the *opposite side* of the body. If care is taken to localise the stimulation as far as possible within the limits of a small area of the cortex the resulting movements are found to be limited to a correspondingly small group of muscles of the limb affected. Again, if that piece of cortex whose stimulation gives rise to movements be cut out or extirpated, the animal so operated on is found to have lost the power of executing this particular set of movements. The outcome of such experiments makes it clear that the cerebral cortex along the course of the fissure of Rolando is concerned in the development of muscular movements; hence the name of "motor areas" was given to these parts of the cortex. Our knowledge of the existence and position of these areas as derived from experiments on animals is moreover completely confirmed by the observation of the results of Nature's own experiments on man; as for instance by an examination after death of the brains of patients who during life had, as the result of cerebral disease, exhibited symptoms similar to those obtainable by stimulation or extirpation of cortical areas in animals.

Proceeding in a similar way it has been further found that certain portions of the cortex are peculiarly connected with the development of sensations, so that we come to speak also of "sensory areas." In this case observations on man are specially instructive, since the patient can give an account of his sensations, whereas another animal cannot.

One of the earliest known and most interesting cases of localisation of function in the cerebral cortex is that of the centre for speech. Some long time before experiment revealed the existence and position of the centres to which we have so far referred it was noticed by a French physician named Broca that patients who had exhibited a curious inability to pronounce definite words or syllables

during life were found after death to have suffered from disease or injury of the *third frontal convolution* of the *left*

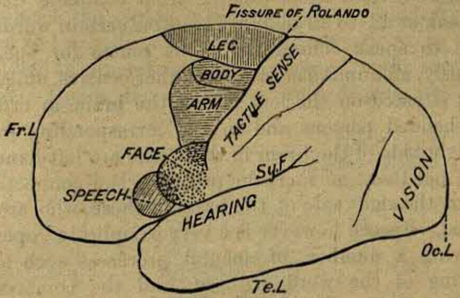


FIG. 170.—DIAGRAM OF OUTER SURFACE OF RIGHT CEREBRAL HEMISPHERE TO SHOW THE POSITION OF CORTICAL AREAS.

The areas for the leg, arm, and face are marked by vertical lines, horizontal lines, and dots respectively. The area for speech lies really in a similar position on the *left* hemisphere.

Fr.L. frontal lobe; *Oc.L.* occipital lobe; *Te.L.* temporal lobe; *Sy.F.* fissure of Sylvius.

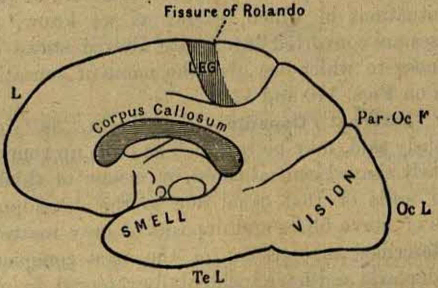


FIG. 171.—DIAGRAM OF INNER (MESIAL) SURFACE OF THE RIGHT CEREBRAL HEMISPHERE TO SHOW THE POSITION OF CORTICAL AREAS.

The *corpus callosum* is seen shaded in section.

Fr.L. frontal lobe; *Oc.L.* occipital lobe; *Te.L.* temporal lobe; *Par-Oc.F.* parieto-occipital fissure.

side of the brain immediately above the Sylvian fissure; hence, this part of the cortex is known as Broca's con-

volution (see Fig. 170). The disorder is, from its nature, known as **aphasia** (*α*, privative of, *φάσις*, speech) and may take several forms ranging from complete inability to speak at all to an inability to utter certain words, and hence to speak coherently. This centre for speech is curiously, and unlike most of the other centres, unilateral, being situated on the left side of the brain in ordinary right-handed persons and in the corresponding part of the right side of the brain in those who are left-handed.

We need say no more in proof of the connection of part of the right side of the brain in those who are left-handed. Speech however is a very complicated operation involving a number of mental processes such as the thinking of the words to say, and the command of muscular movements for their production. Broca's area is probably involved in the latter and is by no means the only portion of the brain involved in speech.

The portion of the brain concerned with tactile sensation is close to the motor areas, being situated just behind, instead of just in front of the fissure of Rolando. The situations in which, so far as we know, afferent impulses are converted into those altered states of consciousness to which we give the name of sensations are shown on Figs. 170 and 171.

The Internal Capsule.—The brain, as we have previously said, may be regarded as built up round a very peculiarly shaped central canal by means of thickenings of the walls of that canal due to the development of masses of nerve fibres and deposits of grey matter. We have described the position of the most conspicuous of these deposits and have incidentally referred to many of the more important inter-connections of the chief parts of which the brain as a whole consists. Moreover, we have referred in some detail to the nature of the connection of the spinal cord with the brain by means of very definite "tracts" of fibres. Among these, particular stress was laid on that tract which is known as the (crossed) pyramidal tract, and it was pointed out (p. 492) that the

fibres of this tract really start in, and depend for their nutrition upon, the cells of the cortex of the cerebral hemispheres. But this dependence is not extended to the cells of the cortex generally; on the contrary it is limited to the cells of those parts of the cortex to which we applied the expression "motor areas," in the preceding section. Hence the pyramidal tract degenerates when

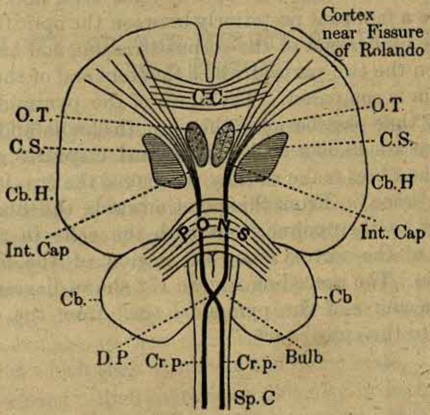


FIG. 172.—DIAGRAM OF THE COURSE OF THE CROSSED PYRAMIDAL TRACT FROM THE (MOTOR) CEREBRAL CORTEX TO THE SPINAL CORD.

C.C. corpus callosum; *O.T.* optic thalamus; *C.S.* corpus striatum; *Int. Cap.* internal capsule; *Cb*, cerebellum; *D.P.* decussation of the pyramids; *Cr.p.*, *Cr.p.* crossed pyramidal tracts (see Fig. 156); *Sp.C.* spinal cord.

the cells of the "motor" areas are destroyed, and thus we come to regard the pyramidal tract as the path by which the (motor) impulses developed in the cortex are distributed to the cells of the spinal cord as a preliminary to their exit from the cord along the anterior roots of the spinal nerves. We traced the pyramidal tract into the bulb, and now we may, in conclusion, follow its further course until its fibres make connection with the cerebral cortex.

When this tract is traced forwards above the bulb it is found to pass into the crus cerebri of its own side and to pass along the lower or ventral part of the crus, which is known as the **pes.** The optic thalami and corpora striata are, as we have seen (p. 508), deposits on the course of the crura as the latter sweep forward into the hemispheres. Now when the fibres of the pyramidal tract reach the level of the thalamus they *rise up out of the crus*, and, spreading like a fan, pass posteriorly between the optic thalamus and the hinder end of the corpus striatum, and anteriorly between the two parts of which the front end of the corpus striatum is composed. The fibres of the pyramidal tract as they thus pass between the optic thalamus and corpus striatum are known as the **internal capsule**, and the bend the fibres make as they rise out of the crus is known as its "knee." From this point onwards the fibres pass directly to their connections with the cells in the grey matter of the cortex along the region of the fissure of Rolando. The preceding Figure 172 shows diagrammatically the course of the pyramidal tract from the cerebral cortex to the spinal cord.

LESSON XII

HISTOLOGY; OR, THE MINUTE STRUCTURE OF THE TISSUES

1. The Body built up of Tissues and the Tissues of Cells.—In the first chapter attention was directed to the obvious fact that the substance of which the body of a man or other of the higher animals is composed, is not of uniform texture throughout; but that, on the contrary, it is distinguishable into a variety of components which differ very widely from one another, not only in their general appearance, their colour, and their hardness or softness, but also in their chemical composition, and in the properties which they exhibit in the living state.

In dissecting a limb there is no difficulty in distinguishing the bones, the cartilages, the muscles, the nerves and so forth from one another; and it is obvious that the other limbs, the trunk, and the head, are chiefly made up of similar structures. Hence, when the foundations of anatomical science were laid, more than two thousand years ago, these "like" structures which occur in different parts of the organism were termed *homoiomera*, "similar parts." In modern times they have been termed *tissues*, and the branch of biology which is concerned with the investigation of the nature of these tissues is called *Histology*.

Histology is a very large and difficult subject, and this whole book might well be taken up with a thorough discussion of even its elements. But physiology is, in

ultimate analysis, the investigation of the vital properties of the histological units of which the body is composed. And even the elements of physiology cannot be thoroughly comprehended without a clear apprehension of the nature and properties of the principal tissues.

A good deal may be learned about the tissues without other aid than that of the ordinary methods of anatomy, and it is extremely desirable that the student should acquire this knowledge as a preliminary to further inquiry. But the chief part of modern histology is the product of the application of the microscope to the elucidation of the minute structure of the tissues; and this has had the remarkable result of proving that these tissues themselves are made up of extremely small *homoiomera*, or similar parts, which are primitively alike in form in all the tissues.

Every tissue therefore is a compound structure: a multiple of histological units, or an aggregation of histological elements; and the properties of the tissue are the sum of the properties of its components. The distinctive character of every fully formed tissue depends on the structure, mode of union, and vital properties of its histological elements when they are fully formed.

2. **The Primitive Tissues.**—Each tissue can be traced back to a young or embryonic condition, in which it has no characteristic properties, and in which its histological elements are so similar in structure, mode of union, and vital properties to those of every other embryonic tissue, that our present means of investigation do not enable us to discover any difference among them.

These embryonic, *undifferentiated*, histological elements, of which every tissue is primitively composed, or, as it would be more correct to say, which, in the embryonic condition, occupy the place of the tissues, are technically named **nucleated cells**. The colourless blood corpuscle (Lesson III., p. 100) is a typical representative of such a cell. And it is substantially correct to say (1) that the histolo-

gical elements of every tissue are modifications or products of such cells; (2) that every tissue was once a mass of such cells more or less closely packed together; and (3) that the whole embryonic body was at one time nothing but an aggregation of such cells.

3. The Body starts as a Single Cell, the Ovum, which then divides into primitive cells.—The body of a man or of any of the higher animals commences as an ovum or egg. This (Fig. 173) is a minute transparent spheroidal sac 200μ, ($\frac{1}{120}$ of an inch) in diameter in man, which contains a similarly spheroidal mass of protoplasm, in which a single large nucleus is imbedded.

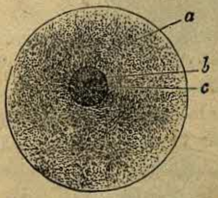


FIG. 173.—DIAGRAM OF THE OVUM.

a, granular protoplasm; *b*, nucleus, called "germinal vesicle"; *c*, nucleolus, called "germinal spot."

The first step towards the production of all the complex organisation of a mammal out of this simple body is the division of the nucleus into two new nuclei which recede from one another, while at the same time the protoplasmic body becomes separated, by a narrow cleft which runs between the two nuclei, into two masses, or *blastomeres* (Fig. 174, *a*), one for each nucleus. By the repetition of the process the two blastomeres give rise to four, the four to eight, the eight to sixteen, and so on, until the embryo is an aggregate of numerous small blastomeres, or nucleated cells. These grow at the expense of the nutriment supplied from without, and continue to multiply by division according to the tendencies inherent in each until, long before any definite tissue has made its appearance, they build themselves up into a kind of sketch model of the developing animal, in which model many of, if not all the future organs, are represented by mere aggregates of undifferentiated cells.

4. The Differentiation of the Primitive Cells.—Gradually, these undifferentiated cells become changed into groups or sets of differentiated cells, the cells in one set being like each other, but unlike those of other sets. Each set of differentiated cells constitutes a "tissue," and each tissue is variously distributed among the several

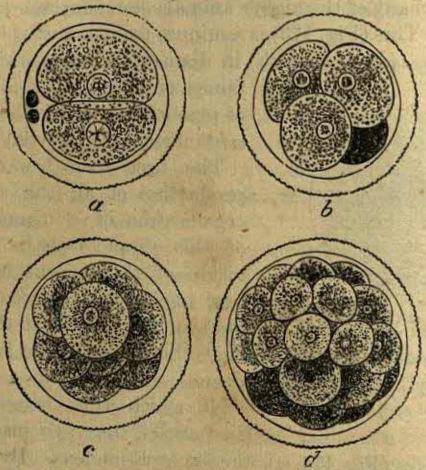


FIG. 174.—THE SUCCESSIVE DIVISION OF THE MAMMALIAN OVUM INTO BLASTOMERES. Somewhat diagrammatic.

a, division into two, *b*, into four, *c*, into eight, and *d*, into several blastomeres. The clear ring seen in each case is the *zona pellucida*, or membrane investing the ovum.

organs, each organ generally consisting of more than one tissue.

And this differentiation of structure is accompanied by a change of properties. The undifferentiated cells are, as far as we can see, alike in function and properties as they are alike in structure. But coincident with their differentiation into tissues, a division of labour takes

place, so that in one tissue the cells manifest special properties and carry on a special work; in another they have other properties, and other work; and so on.

5. The Chief Tissues of the Body.—The principal tissues into which the undifferentiated cells of the embryo become differentiated, and which are variously built up into the organs and parts of the adult body, may be arranged as follows.

(i) The most important tissues are the **muscular** and **nervous** tissues, for it is by these that the active life of the individual is carried on.

(ii) Next come the **epithelial** tissues, which, on the one hand, afford a covering for the surface of the body as well as a lining for the various internal cavities of the body: and, on the other hand, carry on a great deal of the chemical work of the body, inasmuch as they form the essential part of the various glandular organs of the body.

(iii) The remaining principal tissues of the body, namely the so-called **connective tissue, cartilaginous tissue,** and **osseous** or **bony tissue,** form a group by themselves, being all three similar in their fundamental structure, and all three being, for the most part, of use to the body for their passive rather than for their active qualities. They chiefly serve to support and connect the other tissues.

These principal or fundamental tissues are often arranged together to form more complex parts of the body, which are sometimes spoken of, though in a different sense, as tissues. Thus various forms of connective tissue are built up with some muscular tissue and nervous tissue, to form the blood-vessels of the body (see Lesson II.), which are sometimes spoken of as "vascular-tissue." So again, a certain kind of epithelial tissue, known as "epidermis," together with connective tissue, blood-vessels and nerves, forms the skin or tegumentary tissue; a similar combination of epithelium with other tissues

constitutes the mucous membrane lining the alimentary canal, and also occurs in the so-called "glandular" tissue. The structure of these, as also of muscle and nerve and bone, has been already described, so that we may confine our attention here to the other principal tissues; epithelial tissues, the connective tissues and cartilage.

6. **The Epidermis.**—A good example of this tissue is to be found in the skin, which, as we have seen (Lesson V.), consists of the superficial epidermis which is non-vascular and epithelial in nature, and of the deep dermis, which is vascular, and is indeed chiefly composed of connective tissue carrying blood-vessels and nerves. And in all the mucous membranes there is a similar superficial epithelial layer, which is here simply called epithelium, and a deep layer, which similarly consists of connective tissue carrying blood-vessels and nerves and may also be spoken of as dermis.

If a piece of fresh skin is macerated for some time in water, it is easy to strip off the epidermis from the dermis.

The outer part of the epidermis which has been detached by maceration will be found to be tolerably dense and coherent, while its deep or inner substance is soft and almost gelatinous. Moreover, this softer substance fills up all the irregularities of the surface of the dermis to which it adheres, and hence, where the dermis is raised up into papillæ, the deep or under surface of the epidermis presents innumerable depressions into which the papillæ fit, giving it an irregular appearance, somewhat like a network. Hence it used not unfrequently to be called the network of Malpighi (*rete Malpighii*), after a great Italian anatomist of the seventeenth century, who first properly described it. On the other hand, its soft and gelatinous character led to its being called mucous layer (*stratum mucosum*). Chemical analysis shows that the firm outer layer of the epidermis differs from the deep soft part by containing a great deal of horny matter.

Hence this is distinguished as the *horny* layer (*stratum corneum*).

In the living subject the superficial layers of the epidermis become separated from the lower layers and the dermis, when friction or other irritation produces a "blister." Fluid is poured out from the vessels of the derma, and, accumulating between the upper and lower layers of the epidermis, detaches the latter.

The epidermis is constantly growing upon the deep or dermic side in such a manner that the horny layer is continually being shed and replaced. The "scurf" which collects between the hairs and on the whole surface of the body, and is removed by our daily brushing and washing, is nothing but shed epidermis. When a limb has been bandaged up and left undisturbed for weeks, as in case of a fracture, the shed epidermis collects on the surface of the skin in the shape of scales and flakes, which break up into a fine white powder when rubbed. Thus we "shed our skins" just as snakes do, only that the snake sheds all his dead epidermis as a coherent sheet at once, while we shed ours bit by bit, and hour by hour.

What is the nature of the process by which the epidermis is continually removed?

If a little of the epidermic scurf is mixed with water and examined under a power magnifying 300 or 400 diameters, it will seem to consist of nothing but irregular particles of very various sizes and with no definite structure. But if a little caustic potash or soda is previously added to the water the appearance will be changed. The caustic alkali causes the horny substance to swell up and become transparent; and this is now seen to consist of minute separable plates, some of which contain a rounded body in the interior of the plate, though in many this is no longer recognisable. In fact, so far as their form is concerned, these bodies have the character of nucleated cells, in which the protoplasmic

body has been more or less extensively converted into horny substance.

Thus the cast-off epidermis in reality consists of more or less coherent masses of cornified nucleated cells.

There is a yet simpler method of demonstrating this truth. At the margins of the lips the epidermis is continued into the interior of the mouth, and though it now receives the name of epithelium it differs from the rest of the skin in no essential respect except that it is very thin, and allows the blood in the vessels of the subjacent dermis to shine through. Let the lower lip be turned down, its surface very gently scraped with a blunt-

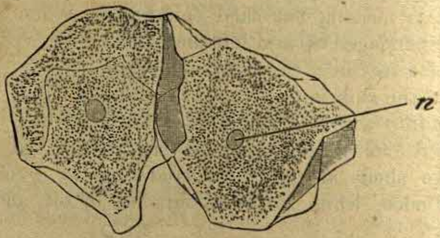


FIG. 175.—TWO EPITHELIAL SCALES FROM THE INTERIOR OF THE MOUTH.

A small nucleus *n* is seen in each, as well as fine granulations in the body of the plate. The edges of the plates are irregular from pressure. Magnified about 400 times.

edged knife, and the substance removed be spread out, and covered with a thin glass, and examined as before. The whole field of view will then be seen to be spread over with flat irregular bodies very like the epidermic scales, but more transparent, and each provided with a nucleus in its centre (Fig. 175).

Since these detached scales are always to be found on the inner surface of the lip, it follows that they are always being thrown off.

7. **The Growth of the Epidermis.**—The horny external layer of the epidermis is composed of coherent

cornified flattened cells, which are constantly becoming detached from the soft internal layer, and must needs be, in some way, derived from it. But in what way? Here microscopic investigation furnishes the answer. For if the soft layer is properly macerated it breaks up into small masses of nucleated protoplasmic substance, that is, into nucleated cells which in the innermost or deepest part of the layer are columnar in form, being elongated perpendicularly to the face of the dermis, on which they rest, and which in the intermediate region present transitions in form and other respects between these and the shed scales.

A thin vertical section of epidermis (see Fig. 57, p. 191) in undisturbed relation with the subjacent dermis, leaves not the smallest doubt (*a*) that the epidermis consists of nothing but nucleated cells, with perhaps an infinitesimal amount of cementing substance between them; (*b*) that from the deep to the superficial part of the dermis, the cells always present a succession from columnar or sub-cylindrical protoplasmic forms to flattened completely cornified forms. And since we know that the latter are constantly being thrown off, it follows (*c*) that these gradations of form represent cells of the deep layer which are continually passing to the surface, and being thrown off there.

What is the cause of this constant succession? To this question, also, microscopic investigation furnishes a clear answer. The deeper cells are constantly growing and then multiplying by a process of division in such a manner that the nucleus of a cell divides into two new nuclei, around each of which one half of the protoplasmic body disposes itself. Thus one cell becomes two, and each of these grows until it acquires its full size at the expense of the nutritive matters which exude from the vessels with which the dermis is abundantly supplied; such a cell in fact possesses the vital properties of a primitive embryo cell.

The cells nearer the dermis are more immediately and abundantly supplied with nourishment from the dermal blood-vessels, and serve as the focus of growth and multiplication for the whole epidermis; they are in fact the progenitors of the superficial cells which, as they are thrust away by the intercalation of new cells between the last formed and the progenitors, become metamorphosed in form and chemical character, and at last die and are cast off.

And it follows that the epidermis is to be regarded as a compound organism made up of myriads of cells, each of which follows its own laws of growth and multiplication, and is dependent upon nothing save the due supply of nutriment from the dermal vessels. The epidermis, so far, stands in the same relation to the dermis as does the turf of a meadow to the subjacent soil.

8. The Unit used in Histological Measurement.—Structures which are rendered clearly distinguishable only by a magnifying power of 300 or 400 diameters must needs be very small, and it is desirable that, before going any further, the learner should try to form a definite notion of their actual and relative dimensions by comparison with more familiar objects. A hair of the human head of ordinary fineness has a diameter of about $\frac{1}{300}$th (say 0·003) of an inch, or 0·08 mm. (millimeter). The hairs which constitute the fur of a rabbit, on the other hand, are very much finer, and the thickest part of the shaft usually does not exceed $\frac{1}{1000}$th of an inch, *i.e.* 0·001 inch, or about 0·025 mm.; while the fine point of such a hair may be as little as $\frac{1}{25000}$th of an inch, about 0·001 mm., or even less in diameter.

In microscopic histological investigations the range of the magnitudes with which we have to deal ordinarily lies between 0·1 and 0·001 millimeter; that is to say roughly between one two hundred and fiftieth and one twenty-five thousandth of an inch. It is therefore extremely convenient to adopt, as a unit of measurement, 0·001

millimeter, called a micro-millimeter, and indicated by the symbol μ, of which all greater magnitudes are multiples.[1] Thus, if the extreme point of a rabbit's hair has a diameter of 1μ, the middle of the shaft will be 25μ, and the shaft of a human head hair 80μ.

Adopting this system, the deep cells of epidermis have on an average a diameter of 12μ or more, the nuclei of 4μ to 5μ, while the superficial cells are plates of about 25μ, the nuclei retaining about the same dimensions. The diameter of a white corpuscle of the blood is about 10μ, that of a red corpuscle being 7μ to 8μ. Hence the deep cells of the epidermis are rather larger than white blood corpuscles, and the uppermost ones much larger, at least in superficial area.

9. The Epithelium of Mucous Membrane.—The mucous membrane lining the alimentary canal, as has been stated, is framed on the plan of the skin, inasmuch as it consists of a vascular dermis, and a non-vascular epithelium, the latter being composed of cells in juxtaposition. But except in the region of the mouth, where, as we have seen, the epithelium, like the epidermis, is composed of many layers of cells, arranged as a soft Malpighian layer and a hard corneous layer, and the œsophagus where the structure is similar, the epithelium of the alimentary canal and the continuations of that epithelium into the ducts and alveoli of the various glands, consists of hardly more than a single layer of cells placed side by side. Hence in a vertical section of the mucous membrane the vascular part is seen to be covered by a single row of soft nucleated cells; though sometimes a second row of inconspicuous small cells may be seen below the latter. The cells constituting this single layer vary in shape, being cylindrical or conical or, as especially in the glands, cubical or spheroidal; but they always are delicate masses of protoplasm, each containing a nucleus.

[1] Since 1 millimeter is very nearly equal to $\frac{1}{25}$ of an inch, $\mu = \frac{1}{25000}$ of an inch.

The polygonal hepatic cells (see p. 212), are in reality the epithelium cells belonging to the minute biliary canals passing between them.

In the trachea and bronchi, the epithelium of the mucous membrane consists again of a single layer of cells, which are cylindrical in form and ciliated. In the ureter and bladder, on the other hand, the epithelium consists of several layers of cells which are frequently irregular in form.

Lastly, the blood-vessels and lymphatic vessels and the large serous cavities, such as the peritoneal and pleural cavities, are lined by a peculiar epithelium, different in origin from the epithelium of the skin and mucous membranes. It consists of a single layer of flat, nucleated plates cemented together at their edges. The form of the plate or cell varies, being sometimes polygonal, sometimes spindle-shaped, sometimes quite irregular (see Fig. 29).

10. The Structure of Cartilage.—A second group of tissues, of which cartilage may be taken as the simplest form and the type, differs from epithelium in a very essential feature. In epithelium, wherever it is found, the cells are placed close together, and the amount of material existing between the cells or *intercellular material* is exceedingly small. In the group of tissues, however, to which cartilage belongs, a very considerable quantity of intercellular material is, as we shall see, developed between the individual nucleated protoplasmic cells. Hence the cells are, more or less, distinctly imbedded in a substance different from themselves and called a *matrix*. In epithelium, though the cells are sometimes joined together by a cement material, this is never abundant enough to deserve the name of matrix.

(i) **Hyaline Cartilage.**—Characteristic specimens of this tissue are to be found in the "sterno-costal cartilages," which unite many of the ribs with the breastbone. A thin but tough layer of vascular connective tissue invests,

and closely adheres to, the surface of the cartilage. It is termed the **perichondrium.** The substance of the cartilage itself is devoid of vessels; it is hard, but not very brittle, for it will bend under pressure; and moreover it is elastic, returning to its original shape when the pressure is removed. It may be easily cut into very thin slices, which are as transparant as glass, and to the naked eye appear homogeneous. Dilute acids and akalies have no effect upon it in the cold; but if it is boiled in water, it yields a substance similar to gelatin, but somewhat different from it, which is called **chondrin.**

The sterno-costal cartilages of an adult man are many times larger than those of an infant. It follows that these cartilages must grow. The only source from whence they can derive the necessary nutritive material is the plasma exuded from the blood contained in the vessels of the perichondrium. The vascular perichondrium therefore stands in the same relation to the non-vascular cartilaginous tissue as the vascular dermis does to the non-vascular epidermis. But, since the cartilage is invested on all sides by the perichondrium, it is clear that no part of the cartilage can be shed in the fashion that the superficial layers of epidermis are got rid of. As the nutritive materials, at the expense of which the cartilage grows, are supplied from the perichondrium, it might be concluded that the cartilage grows only at its surface. But if a piece of cartilage is placed in a staining fluid, it will be found that it soon becomes more or less coloured throughout. In spite of its density, therefore, cartilage is very permeable, and hence the nutritive plasma also may permeate it, and enable every part to grow.

If a thin section of perfectly fresh and living cartilage is placed on a glass slide, either without addition or with only a little serum, it appears to the naked eye, as has been said, to be as homogeneous as a piece of glass. But the employment of an ordinary hand magnifier is sufficient

to show that it is not really homogeneous, inasmuch as minute points of less transparency are seen to be scattered singly or in groups throughout the thickness of the section. When the section is examined with the microscope (Fig. 176) these points prove to be nucleated cells, **the cartilage corpuscles**, varying in shape, but generally more or less spheroidal, sometimes far apart, sometimes very near, or in groups in contact with one another, in which last case the applied sides are flat. Usually each cell has a single nucleus, but sometimes there are two nuclei in a cell. And sometimes globules

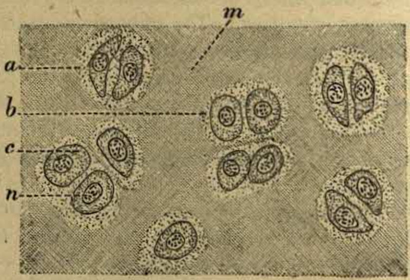


FIG. 176.—HYALINE CARTILAGE. A THIN SECTION HIGHLY MAGNIFIED.
m, matrix; *a*, group of two cartilage cells; *b*, a group of four cells; *c*, a cell; *n*, nucleus.

of fat appear in the protoplasmic bodies of the cells, and may completely fill them.

As a rule each cell lies in, and exactly fills, a cavity in the transparent **matrix**, or **intercellular substance**, which constitutes the chief mass of the tissue. But a pair of closely opposed flattened cells may occupy only one cavity, and all sorts of gradations may be found between hemi-spheriodal cells in contact, and hemi-spheriodal cells separated by a mere film of intercellular substance, and widely separate spheroidal, ellipsoidal, or otherwise shaped

cells. In size, the cells vary very much, some being as small as 10μ, and others as large as 50μ, or even larger.

As the cartilage dies, and especially if water is added to it, the protoplasmic bodies of the cells shrink and become irregularly drawn away from the walls of the cavities which contain them, and the appearance of the tissue is greatly altered.

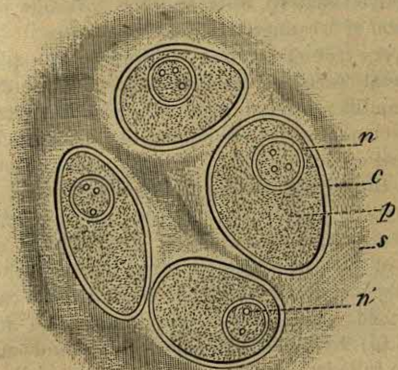


FIG. 177.—A SMALL PORTION OF A SECTION OF ARTICULAR CARTILAGE (FROG) VERY HIGHLY MAGNIFIED (600 diam.).

s, matrix or intercellular substance; *p*, the protoplasmic body of the cartilage corpuscle; *n*, its nucleus, with *n'*, nucleoli; *c*, the capsule, or wall of the cavity in which the cartilage corpuscle lies. The four cells here figured seem to have arisen from a single cell, by division, first into two and then into four. The shading of the matrix in an oblique line indicates the earlier division into two.

No structure is discernible in the matrix or intercellular substance under ordinary circumstances; but it may be split up into thin sheets or laminæ. The portions of matrix immediately surrounding the several cavities sometimes differ in appearance and nature from the rest of the matrix, so as to constitute distinct **capsules** (Fig.

177, *c*) for the cells; and, at times, the matrix may by appropriate methods be split up into pieces, each belonging to and surrounding a cell, or group of cells, and often disposed in concentric layers.

Close to the perichondrial surface of the cartilage the cells become smaller and separated by less intercellular substance, until at length the transparent chondrigenous material is replaced by the fibrous collagenous substance of connective tissue (p. 554), and the cartilage cells take on the form of "connective tissue corpuscles."

In a very young embryo we find in the place of a sterno-costal cartilage nothing but a mass of closely-applied, undifferentiated, nucleated cells, having the same essential characters as colourless blood-corpuscles, or as the deepest epidermic cells. The rudiment, or embryonic model of the future cartilage thus constituted, increases in size by the growth and division of the cells. But, after a time, the characteristic intercellular substance appears, at first in small quantity, between the central cells of the mass, and a delicate sterno-costal cartilage is thus formed. This is converted into the full-grown cartilage (*a*) by the continual division and subsequent growth to full size, of all its cells, and especially of those which lie at the surface; (*b*) by the constant increase in the quantity of intercellular substance, especially in the case of the deeper part of the cartilage.

The manner in which this intercellular substance is increased is not certainly made out. If the outermost layer only of each of the protoplasmic bodies of adjacent cells of the epidermis were to become cornified and fused together into one mass, while the remainder of each cell continued to grow and divide and its progeny threw off fresh outer cornified layers, we should have an epidermic structure which would resemble cartilage except that the "intercellular substance" would be corneous and not chondrigenous. And it is possible that the intercellular substance of cartilage may be formed in this

way. But it is possible that the chondrigenous material may be, as it were, secreted by and thrown out between the cells, as the constituents of the bile are thrown out between the hepatic cells, or at all events manufactured in some way by the agency of the cells, without the substance of the cells being actually transformed into it. Thus the capsule of each cell may be such a secretion, which then fuses into the adjacent matrix. Our knowledge will not at present permit us to form a definite judgment on this point. One thing, however, seems certain, viz. that the cells are in some way concerned in the matter; the matrix is unable to increase itself in the entire absence of cells.

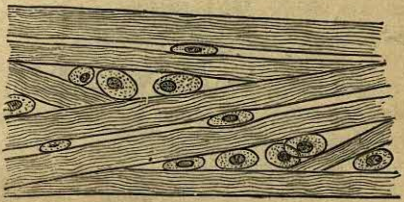


FIG. 178.—SECTION OF WHITE FIBRO-CARTILAGE. (HARDY.)

The embryonic cells, which give rise to cartilage, are not distinguishable by any means we at present possess in any respect of importance from those which give rise to epidermis.

Nevertheless, the common form must disguise a different molecular machinery, inasmuch as the two, when set going by the conditions of temperature, supply of oxygen and nutriment to which they are exposed in the living economy, work out, as their ultimate products, tissues which differ so widely as cartilage and epidermis.

The embryonic cartilage cells, like the embryonic epidermic cells, are living organisms in which certain

definitely limited possibilities of growth and metamorphosis are inherent, as they are in those equally simple organisms, the spores of the common moulds, *Penicillium* and *Mucor*. Given the proper external conditions, the latter grow into moulds of two different kinds, while the former grow into cartilage and horny plates.

(ii) **White Fibro-Cartilage.**—Since cartilage is a tissue which serves chiefly for the purposes of supporting and connecting other structures of the body, it requires, in certain positions, to be somewhat more tough and resistent, less brittle and more flexible than in others. Thus in some joints, as for instance the knee, there are little pads or discs of cartilage between the ordinary

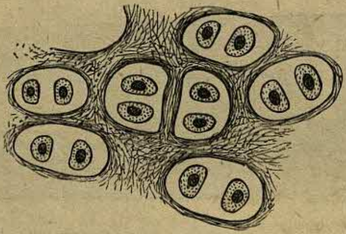


FIG. 179.—SECTION OF YELLOW ELASTIC CARTILAGE. (HARDY.)

articular cartilage (see Fig. 97, *c*). Similar discs lie in between and are attached to the bodies of the vertebræ. They act not only as a sort of cushion to break the "jar" arising from a sudden concussion of the vertebral column, but also bind the vertebræ into a column which is resistent but at the same time flexible. The additional strength required by the cartilages of these discs is provided by the introduction into their matrix of bundles of white fibrous connective tissue; hence the name, white fibro-cartilages (Fig. 178).

(iii) **Yellow or Elastic Fibro-Cartilage.**—In certain other parts of the body cartilage is required to be pecu-

liarly elastic and flexible, as in the epiglottis and cartilage of the external ear. In this case the requisite elasticity is given to it by the introduction into the matrix of a dense feltwork of fibres of yellow or elastic connective tissue (Fig. 179).

11. The Connective Tissues.

(i) **Areolar Tissue.**—If a specimen of the loose subcutaneous tissue which binds the skin to the body or of the similar tissue from between the muscles of a limb, be examined, it is found to be a soft stringy substance, which, if a small portion is carefully spread out in fluid on a glass slide and examined without the aid of any microscope, is seen to consist of semi-transparent whitish bands and fibres, of very various thicknesses, interlaced so as to form a network, the meshes of which are extremely irregular. Hence the older anatomists termed this tissue **areolar** or *cellular*.

Boiled in water, the connective tissue swells up and yields gelatin, which sets into a jelly as the water cools. After prolonged boiling, especially under pressure, it almost entirely dissolves away into gelatin, only a small filamentous solid residue remaining behind.

Dilute acids and dilute alkalies also cause connective tissue to swell up and acquire a glassy transparency, but they do not dissolve it. For if to a portion of the tissue thus altered by either acid or alkali, alkali or acid is added sufficient to neutralise the first, the tissue returns to its normal condition.

If a specimen thus rendered transparent by dilute acetic acid is examined with a magnifying glass, fine dark lines and dots are seen to be scattered through the apparently homogeneous substance. Placed under the microscope, the lines are seen to be sharply defined fibres of a strongly refracting substance. They are very elastic and are unaffected by even strong acids or alkalies or by prolonged boiling. Hence these **elastic fibres** formed a considerable part of the residue above mentioned.

The dots seen with the magnifying glass are shown by the microscope to be small nucleated cells. They are termed **connective tissue corpuscles**, just as cartilage cells are called *cartilage corpuscles.*

Thus, connective tissue resembles cartilage in so far as it consists of cells separated by a large quantity of intercellular substance; but this intercellular substance is soft, areolated fibrous, and, for the most part, either

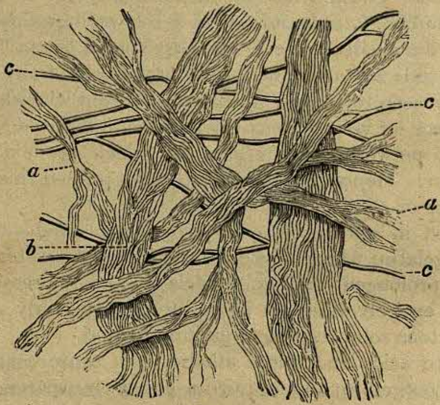


FIG. 180.—CONNECTIVE TISSUE FIBRES.

a, small bundles of white fibrous tissue; *b*, larger bundles; *c*, single elastic fibres.

collagenous or elastic, in contradistinction from that of cartilage, which is hard, solid, laminated and chondrigenous.

A specimen of fresh connective tissue prepared for the microscope in its own fluid exhibits a very different appearance. The field of view is occupied by strings or threads of extremely various thicknesses which cross one another in all directions and are often wavy. Some of the threads can be recognised as elastic by their strongly

refracting character, but the majority of them are pale and not darkly contoured. All the thicker threads and strings present a fine longitudinal striation as if they were bundles of extremely fine fibrillæ (Fig. 181, A). At intervals such bundles are often encircled by rings of a more refractive substance, and fibres of the like character may be disposed spirally round the bundles.

When dilute acetic acid is added to the specimen, the pale threads and longitudinally striated strings swell up and the longitudinal striation disappears; hence it is that the specimen becomes so transparent (Fig. 181, B). More-

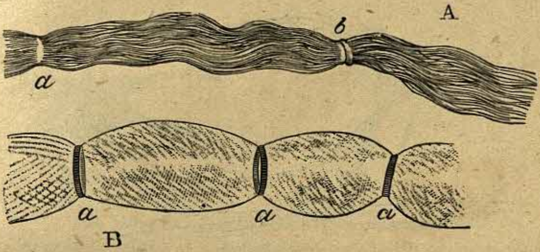


FIG. 181.

A. A small bundle of connective tissue, showing longitudinal fibrillation, and at *a* and *b* encircling (annular, spiral) fibres. Magnified 400 diameters.

B. A similar bundle swollen and rendered transparent by dilute acid. The encircling fibres are seen at *a*, *a*, *a*.

over it is these striated threads and strings which are dissolved by boiling water, and yield gelatin. We may therefore speak of them as **collagenous** or gelatin-yielding fibres, by way of distinction from the fibres of **elastic** substance, which do not yield gelatin on boiling, and are of a different chemical nature.

By various modes of maceration the collagenous fibres may be resolved into filaments which answer to the space between the striæ, and are of such extreme fineness that they may measure less than 1μ in diameter. It

would appear therefore that the intercellular substance of the connective tissue in question is composed of (*a*) **collagenous filaments**, united by some cementing substance into bundles, and of (*b*) **elastic fibres**. These latter are generally united into long meshed networks (Fig. 182).

With care, the *cells* or **connective tissue corpuscles** may also be seen even in fresh, living connective tissue (Fig. 183); but, as has been stated, they are most distinctly visible when the tissue is treated with dilute acetic acid. These cells, when seen in the fresh tissue,

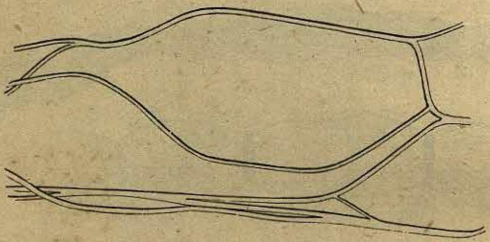


FIG. 182.—ELASTIC FIBRES OF CONNECTIVE TISSUE, FORMING A LOOSE NETWORK.

Obtained by special preparation from subcutaneous tissue. Magnified 800 diameters.

care being taken to prevent the post-mortem changes which they readily undergo, are found to be flattened plates almost like epithelial scales, but with very irregular contours. They closely adhere to, and are, as it were, bent round the convex faces of the larger bundles of collagenous fibres.

Besides these *fixed* connective tissue corpuscles as they are called, white blood corpuscles, or lymph corpuscles, or bodies exceedingly like them, are found lying loose in the fluid which occupies the meshes of the network of fibres, and appear to wander or travel through the spaces of the

network by virtue of their power of amoeboid movement (Lesson III.). Such cells are spoken of as wandering or migratory cells.

Such are the characters of that which may be regarded as a typical specimen of connective tissue. But in different parts of the body this tissue presents great differences, all of which, however, are dependent upon the different relative extent to which the various elements of the tissue are developed.

Thus, (*a*) The intercellular substance may be very much reduced in amount in proportion to the cells, as is the

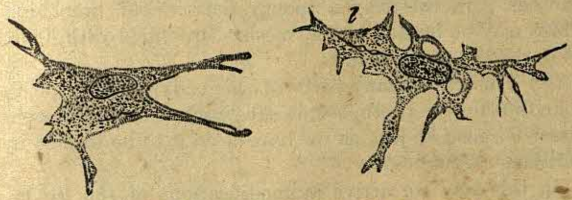


FIG. 183.—TWO CONNECTIVE TISSUE CORPUSCLES.

Each is seen to consist of a protoplasmic branched body, containing a nucleus. Very highly magnified.

case in the superficial layer of the dermis and some other places.

(*b*) The intercellular substance may be abundant, and the collagenous elements, with fibrils strongly marked and arranged in close-set parallel bundles, leaving mere clefts in the place of the wide meshes of ordinary connective tissue. This structure is seen in tendons and most ligaments.

(*c*) The elastic element may predominate as in certain (few) ligaments and the vocal cords.

(*d*) The fibrous or elastic elements may abound, but a greater or less amount of chondrigenous substance is developed around the corpuscles. These are respectively the **fibro-cartilages** and **elastic cartilages**, which we

have already described and which present every transition between ordinary cartilage and ordinary connective tissue (epiglottis, intervertebral ligaments). Where a tendon is inserted into a cartilage, as in the case of the *tendo Achillis*, (Fig. 90), the passage of the cartilage into the tendon is beautifully displayed. The intercellular substance of the cartilage gradually takes on the characters of that of the tendon, and the corpuscles of the cartilage become connective-tissue corpuscles.

(*e*) The intercellular substance may largely disappear and the interlacing bundles of collagenous fibres may actually join together at the points when they cross one another. In this way a spongy network of branching fibres may be formed whose meshes are filled with fluid, as in the lymphatic glands.

(*f*) Finally, in many parts of the body fatty matter is found within the protoplasmic substance of the connective tissue corpuscles just as we have seen it to be formed in cartilage corpuscles.

In this way we arrive at modifications of the fundamental type of connective (areolar) tissue which are so characteristic as to merit separate description.

(ii.) **White Fibrous Tissue.**—This form is met with in the dense and strong connective tissue of which tendons and most ligaments are composed. In these structures the collagenous fibres of areolar tissue are arranged in *dense, parallel bundles*, among which are a certain number of peculiarly flattened connective tissue corpuscles, arranged in rows and now called tendon cells. The structure of a tendon thus provides the qualities so essential to it of great strength, complete flexibility, but absolute want of all elasticity or extensibility.

(iii.) **Yellow Elastic Tissue.**—This form occurs typically in the strong ligament (*ligamentum nuchae*) at the back of the neck (see Fig. 102, *b*) which, while giving support to the head, permits it at the same time to be bent forward, since the ligament is extensible. This ligament

is very highly developed in long-necked animals such as the horse. The vocal cords of the larynx are also composed of this tissue.

It consists of the elastic fibres of areolar tissue, now arranged in dense, more or less *parallel, bundles.* The fibres are sufficiently thick to show a well-marked outline. They also frequently branch into finer fibres, and when teased out the broken ends of the fibres are characteristically curled (Fig. 184).

FIG. 184.—ELASTIC FIBRES TEASED OUT AND MAGNIFIED ABOUT 200 DIAMETERS. (SHARPEY.)

(iv.) **Adenoid, Retiform or Lymphoid Tissue.**—As already described (p. 90) the functionally essential parts of a lymphatic gland are composed of this tissue, and it permeates the "pulp" of the spleen, although here it is in a somewhat modified form.

Adenoid tissue is a simple *network of branching fibres* (see Fig. 30) whose substance is nearly identical with that of the collagenous fibres of areolar tissue, but has some affinities to that of elastic tissue.

(v.) **Adipose Tissue.**—This tissue is the ordinary "fat" found in many parts of the body. It consists simply of areolar connective tissue in which the connective tissue corpuscles are present in vast numbers and contain neutral fat, composed of a mixture of stearin, olein and palmitin. These modified cells are held together by a vascular framework furnished by the connective tissue to which they belong.

The cells are at first indistinguishable from ordinary

connective tissue corpuscles, but by degrees minute granules and droplets of fat appear in the cell-substance, increase in numbers, distend the body of the cell, and

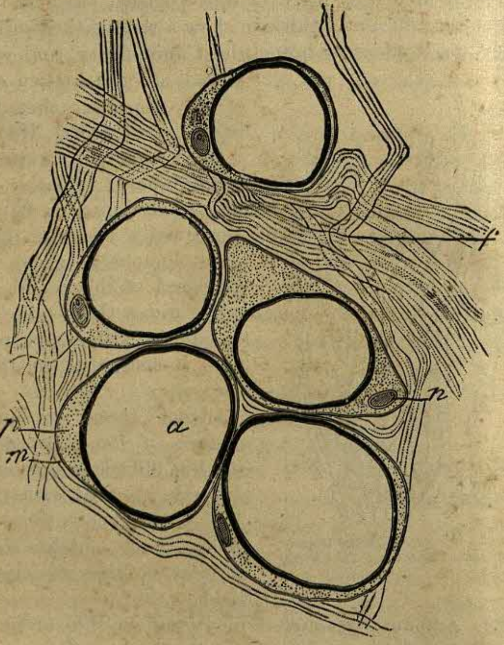


FIG. 185.—ADIPOSE TISSUE.

Five fat cells, held together by bundles of connective tissue f. m, the membrane or envelope of the fat cell; n, the nucleus, and p, the remains of the protoplasm pushed aside by the large oil drop a. Magnified 200 diameters.

take the place of the cell-substance. Thus finally each cell becomes a spheroidal sac full of fat, with the nucleus pushed to one side (Fig. 185).

APPENDIX

ANATOMICAL AND PHYSIOLOGICAL CONSTANTS

THE weight of the body of a full-grown man may be taken at 70 kilogrammes (154 lbs.).

I. GENERAL STATISTICS.

Such a body would be made up of—

	Per cent.	lbs.
Muscles and tendons	42	64·7
Skeleton	16	24·6
Skin	7	10·8
Fat	19	29·3
Brain	2	3·1
Thoracic viscera	2	3·1
Abdominal viscera	7	10·8
Blood[1]	5	7·7
	100	154·1

Or of—

Water	57	88
Solid matters	43	66

[1] The total quantity of blood in the body is calculated at about $\frac{1}{20}$ of the body weight or rather more.

The solids would consist of the elements oxygen, hydrogen, carbon, nitrogen, phosphorus, sulphur, silicon, chlorine, fluorine, potassium, sodium, calcium (lithium), magnesium, iron (manganese, copper, lead), and may be arranged under the heads of—

Proteins. Carbo-hydrates. Fats. Minerals.

Such a body would lose in 24 hours—of water, about 2,600 grammes (6 lbs. or $4\frac{1}{2}$ pints); of other matters, about 940 grammes (2 lbs.), which would contain about 270–300 grammes (or rather more than $\frac{1}{2}$ lb.) of carbon, 20 grammes ($\frac{3}{4}$ oz.) of nitrogen and 30 grammes (about 1 oz.) of mineral matters (inorganic salts).

It could do about 150,000 kilogramme-metres (480 foot-tons[1]) of work, and gives off as much heat (2,300 kilogramme degree units) as would be able to do five times as much work again, say 850,000 kilogramme-metres (or about 2,700 foot-tons). The total energy expended by the body as heat and work (calculated entirely as work) is thus about 1,000,000 kilogramme-metres (3,180 foot-tons), of which one-sixth is expended as work and five-sixths as heat.

The loss of substance would occur through various organs and to the respective amounts shown in the table on p. 268.

The gains and losses of this body would be *about* as follows:—

Creditor:—	Solid dry food	600 grammes	($1\frac{1}{4}$ lbs.)
	Oxygen	640 ,,	($1\frac{1}{2}$,,)
	Water	2,300 ,,	($5\frac{1}{4}$,,)
		3,540 grammes	(8 lbs.)
Debtor:—	Water	2,600 grammes	(6 lbs.)
	Other matters	940 ,,	(2 ,,)
		3,540 grammes	(8 lbs.)

[1] A foot-ton is the equivalent of the work required to lift one ton one foot high.

II. Nutrition.

Such a body would require for daily food, carbon 270–300 grammes, nitrogen 20 grammes.

Now proteins contain, in round numbers, about 15 per cent. nitrogen and 53 per cent. carbon, while carbo-hydrates and fats contain respectively 40 per cent. and 80 per cent. carbon. Hence the necessary amounts of nitrogen and carbon, together with the other necessary elements, might be obtained as follows (see p. 271):—

Proteids	130 grms.	containing	20 grms. nitrogen	70 grms. carbon
Carbo-hydrates	400 ,,	,,	—— ,,	160 ,, ,,
Fats	50 ,,	,,	—— ,,	40 ,, ,,
Minerals	30 ,,	,,	—— ,,	— ,, ,,
Water	2,300 ,,			
	2,910		20	270

This *might* in turn be obtained, for instance, from :—

Lean meat	230	grammes	($\frac{1}{2}$ lb.)
Bread	480	,,	(say 1 lb.)
Potatoes	660	,,	($1\frac{1}{2}$ lb.)
Milk	500	,,	($\frac{3}{4}$ pint)
Fat	30	,,	(1 oz.)
Water	2,300	,,	(4 pints)

This table, however, must be understood as being introduced for the sake of illustration only. Many other similar tables may be constructed by the use of various kinds of food.

III. Circulation.

In such a body the heart would beat about 72 times in a minute and probably drive out at each stroke from each ventricle about 80 grammes (4 cubic inches or 3 ounces) of blood.

The blood would probably move in the great arteries at the rate of about 8 inches (200 millimetres) in a *second* ;

in the capillaries at the rate of 1–2 inches (25–50 millimetres) in a *minute.* The shortest time taken up in performing the complete circuit would probably be about 30 seconds.

The *left* ventricle would probably establish a blood-pressure in the aorta equal to the pressure (per square inch) of a column of blood about 6 feet (1·8 metres) in height; or of a column of mercury 5–6 inches (140 millimetres) in height.

Sending out 80 grammes of blood at each stroke against this pressure the *left* ventricle does 80×1800 gramme-millimetres or 144 gramme-metres of work at each stroke: in 24 hours, at 72 strokes per minute, the total work done is about 15,000 kilogramme-metres. The work of the *right* ventricle is about one quarter of that done by the left, since it works against a smaller blood-pressure in the pulmonary artery. The total work of both ventricles is therefore about 20,000 kilogramme-metres, or 68 foot-tons.

IV. Respiration.

Such a body would breathe about 17 times a minute.

The lungs would contain of residual air about 1,500 c.c. (100 cubic inches), of supplemental or reserve air about 1,500 c.c. (100 cubic inches), of tidal air 500 c.c. (20 to 30 cubic inches), and of complemental air 500 c.c. (100 cubic inches).

The vital capacity of the chest—that is, the greatest quantity of air which could be inspired or expired—would be about 3,500 c.c. (230 cubic inches).

There would pass through the lungs, per diem, about 10,000 litres (350 to 400 cubic feet) of air.

In passing through the lungs, the air would lose from 4 to 6 per cent. of its volume of oxygen, and gain 4 to 5 per cent. of carbonic acid.

During 24 hours there would be consumed of oxygen about 450 litres (16 cubic feet) or 640 grammes ($1\frac{1}{2}$ lb.);

there would be produced about the same volume (or rather less) of carbonic acid, which would contain about 225 grammes (8 ounces) of carbon. During the same time about 250 grammes (half a pint or 9 ounces) of water would be given off from the respiratory organs.

In 24 hours such a body would vitiate 1,750 cubic feet (1 cubic foot = 28·3 litres) of pure air to the extent of 1 per cent., or 17,500 cubic feet of pure air to the extent of 1 per 1,000. Taking the amount of carbonic acid in the atmosphere at 3 parts, and in expired air at 470 parts in 10,000, such a body would require a supply per diem of more than 23,000 cubic feet of ordinary air, in order that the surrounding atmosphere might not contain more than 1 per 1,000 of carbonic acid (when air is vitiated from animal sources with carbonic acid to more than 1 per 1,000, the concomitant impurities become appreciable to the nose). But for health, the percentage of carbonic acid should be kept down to half this amount or ·5 per 1000, so that the body should be supplied with at least about 50,000 cubic feet of fresh air each day. A man of the weight mentioned (11 stone) ought, therefore, to have at least 1,000 cubic feet of well-ventilated space.

V. Cutaneous Excretion.

Such a body would throw off by the *skin*—of water about 650 grammes (23 ounces or 1 pint); of solid matters about 20 grammes (300 grains); of carbonic acid about 25 grammes (400 grains) in 24 hours.

VI. Renal Excretion.

Such a body would pass by the *kidneys*—of water about 1,500 grammes or cubic centimeters (53 ounces or $2\frac{1}{2}$ pints); of urea about 33 grammes (500 grains or $1\frac{1}{4}$ oz.), and about the same quantity of other solid matters in 24 hours.

VII. Nervous Action.

A nervous impulse travels along a nerve at the rate of about 80 feet in a second in the frog, but much more rapidly in man.

VIII. Histology.

The following are some of the most important histological measurements :—

Red blood-corpuscles, breadth $\frac{1}{3200}$th of an inch, or 7 μ to 8 μ.

White blood-corpuscles, breadth $\frac{1}{2500}$th of an inch, or 10 μ.

Striated muscular fibre (very variable), breadth $\frac{1}{400}$th of an inch, or 60 μ ; length $1\frac{1}{2}$ inch, or 30 to 40 millimetres.

Non-striated muscular fibre (variable), breadth $\frac{1}{4000}$th of an inch, or 6 μ ; length $\frac{1}{500}$th of an inch, or 50 μ.

Nerve fibre (very variable), breadth $\frac{1}{12000}$th to $\frac{1}{2000}$th of an inch, or 2 μ to 12 μ.

Nerve cells (of spinal cord) excluding processes, breadth $\frac{1}{500}$th to $\frac{1}{250}$th or more of an inch, 50 μ to 100 μ or more.

Fibrils of connective tissue, breadth $\frac{1}{25000}$th of an inch, or 1 μ.

Superficial cells of epidermis, breadth $\frac{1}{1000}$th of an inch, or 25 μ.

Capillary blood-vessels (variable), with $\frac{1}{3500}$th to $\frac{1}{2000}$th of an inch, or 7 μ to 12 μ.

Cilia, from the wind-pipe, length $\frac{1}{3000}$ of an inch or 8 μ.

Cones in the yellow spot of the retina, width $\frac{1}{8000}$th of an inch, or 3 μ.

INDEX

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